Department of Psychology

AN ANATOMICAL AND BEHAVIORAL ANALYSIS OF

VISUAL CORTEX IN THE HEDGEHOG

by

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Duke University

Date: July 18 1967

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A dissertation submitted in partial fulfillment
of the requirements for the degree of Doctor
of Philosophy in the Department of
Psychology in the Graduate
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ABSTRACT

(Psychology--Physiological)

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The hedgehog was selected for an anatomical and behavioral investigation of the visual system because, in terms of the expansion and internal differentiation of its dorsal thalamus and neocortex, this animal appears to have retained a remarkably primitive level of development. By study of a primitive mammal, the hope was to provide a basis for understanding the phylogenetic significance of the similarities and differences found among higher mammals in the anatomical and functional organization of the visual system.

In the anatomical experiments, the visual cortex was defined in terms of cytoarchitecture; the cortical projections of the lateral geniculate to this region were then studied in fourteen hedgehogs by the method of thalamic retrograde degeneration. The lateral geniculate was found to project

to the cytoarchitectonically defined visual area in a topographic manner. At the same time, individual neurons in the lateral geniculate appeared to have diffuse cortical terminations which included extensive regions of the cortex surrounding the visual area. Thus small lesions in the cytoarchitectonic visual area produced widespread but slight degenerative changes in the lateral geniculate. The severity of the degeneration increased with the size of the cortical removal in this region. The most severe degeneration produced in the lateral geniculate, however, was present only after large lesions which extended considerably beyond the boundaries of the visual area.

The purpose of the behavioral experiments was to determine by means of the ablation method the structural unit for pattern discrimination in the hedgehog. Ten hedgehogs were trained to pattern discrimination problems before and after bilateral cortical ablations. The major finding was that despite the widespread projections of the lateral geniculate, pattern discrimination in the hedgehog after cortical surgery is dependent upon the survival of at least a small remnant of the cytoarchitectonic visual area. Complete removal of this area resulted in a permanent inability to discriminate patterns even if, at the same time,

the ablations spared large portions of the total projection target of the lateral geniculate. The conclusion was that pattern discrimination had become precisely dependent upon this cytoarchitectonic region at an early stage in the evolution of mammals. One can recognize this prototypic organization in species as diverse as the rat and the monkey.

ACKNOWLEDGEMENTS

I wish to express my appreciation to Mrs. Janet Hall for preparing histological materials and photomicrographs and for her help in many other phases of completing the present paper and to Mrs. Stephanie Doetsch for drawing and preparing the illustrations.

I am also grateful to Mr. John Monahan for collecting the normal behavioral data from three of the animals used in the present study.

During the course of these experiments Dr. F. Sanides of the University of Wisconsin began a comprehensive study of the cytoarchitecture of the hedgehog cortex. Dr. Sanides was kind enough to send us some of his preliminary findings concerning the cytoarchitecture of the hedgehog visual cortex. His assistance provided a major step toward the completion of the present experiments.

I would also like to thank Drs. R. P. Erickson, N. Guttman, G. A. Kimble, and T. L. Peele for their respective contributions to my graduate studies and for their willingness to serve on my dissertation committee.

Special acknowledgement goes to Dr. I. T. Diamond who participated in all phases of these experiments. Without

his encouragement and advice the experiments could not have been completed.

W.C.H.

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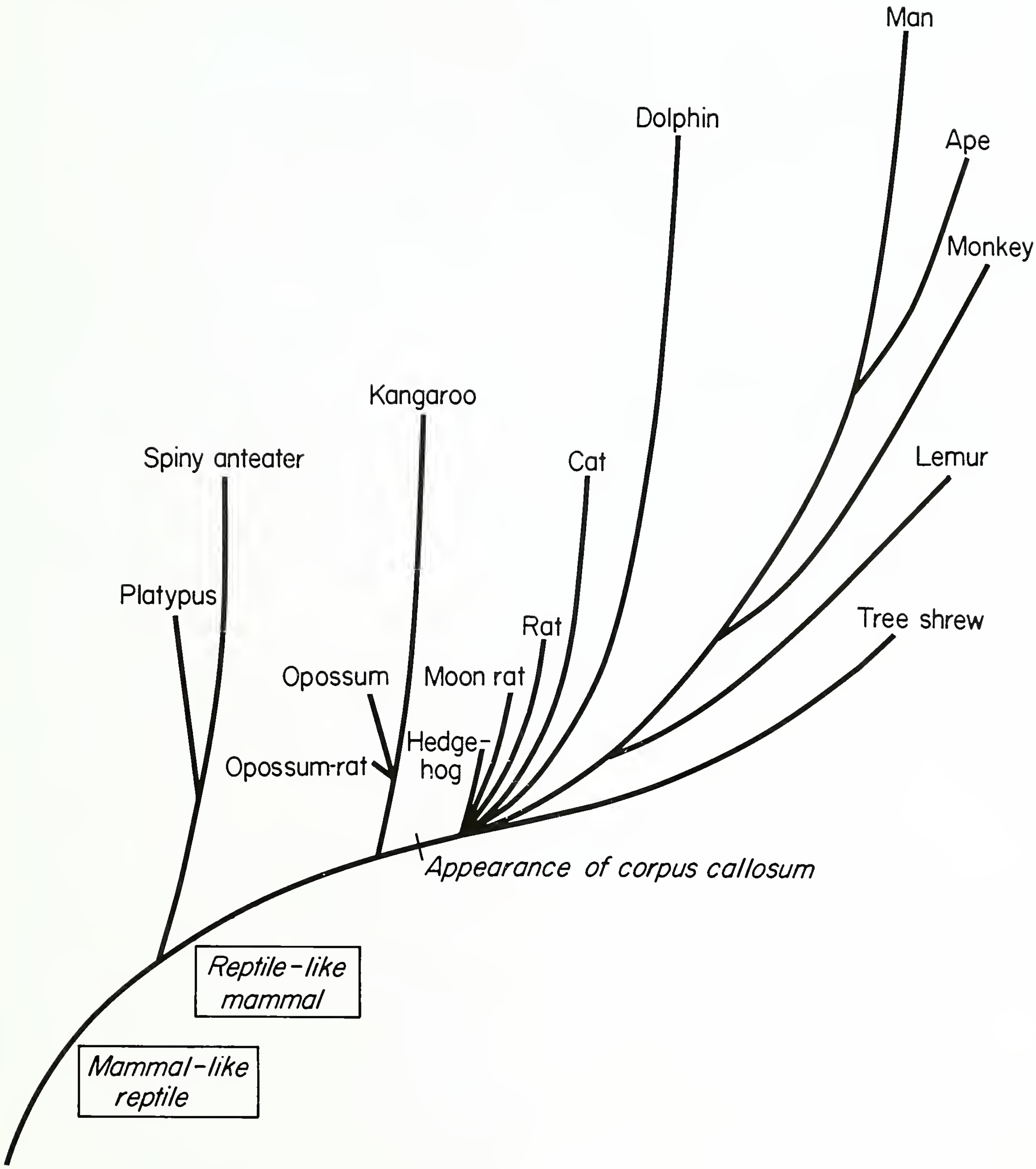
INTRODUCTION

If the dramatic differences in the development of neocortex which distinguish higher and lower mammals are interpreted in terms of the genetic affinities of the species, it becomes evident that this structure evolved into a highly elaborate form many separate times in mammalian phylogeny (Fig. 1). For understanding the anatomical and functional organization of neocortex, it is essential to know the extent to which these independent processes of elaboration followed parallel or divergent courses in each of the various lines of mammalian descent.

Among several mammalian lines, for example, differences have been found in the organization of the cortical visual system. Thus in higher primates, the cortical projection target of the lateral geniculate body is limited to cytoarchitectonically defined striate cortex and correspondingly, removal of the striate area results in a permanent inability to perceive visual patterns (Polyak, 1933; Klüver, 1942; Denny-Brown and Chambers, 1955). In the tree

Figure 1. Diagrammatic Representation of Phylogenetic Development of Neocortex (Diamond, 1967). The Figure shows the genetic affinity of several mammalian species. The height of the lines approximates the development of neocortex relative to old cortex in each of these species. The Figure is intended to show that the expansion of neocortex occurred independently many times in the history of mammals.



Man
Dolphin
Ape
Monkey
Kangaroo
Spiny anteater
Cat
Lemur
Platypus
Rat
Tree shrew
Opossum
Moon rat
Hedge-hog
Opossum-rat
Appearance of corpus callosum
Reptile-like mammal
Mammal-like reptile

shrew, *Tupaia glis*, an animal of uncertain taxonomic status, the striate area also receives the total projection of the lateral geniculate but in contrast to the monkey, this species was found to retain excellent pattern vision after complete striate removal (Snyder, Hall, and Diamond, 1966). The cat may possess still a third organization. Although there is evidence that the cat, like the tree shrew, can perceive patterns after complete ablation of the striate area, the lateral geniculate in this animal has extensive extrastriate projections (Hahn, Diamond, and Neff, 1955; Doty, 1961; Glickstein *et al.*, 1967).

One approach to the problem of the phylogenetic origin and significance of these differences in organization is to study primitive mammals. Thus by turning to species which comparative anatomical considerations indicate have changed relatively little in mammalian evolution, it may be possible to describe an organization of the visual system which closely approximates the level of development actually attained by ancestral mammals. The question of the course of evolution in the different mammalian lines can then be partially answered by comparing the organization of each advanced species with this primitive plan.

In an effort to describe a phylogenetically early organization of the cortical visual system, a series of anatomical and behavioral experiments has been conducted on

a primitive eutherian mammal, the hedgehog. The results of these experiments will be presented in the present paper.

The starting point for the experiments on the hedgehog was a study of thalamo-cortical connections conducted several years ago in this laboratory on a primitive marsupial, the opossum (Diamond and Utley, 1963). The results of this investigation indicated that the relations between the projection targets of the sensory relay nuclei in the thalamus, GM, VP and GL[1] on one hand, and cytoarchitectonically defined cortical regions on the other, may not be the same for higher and lower mammals. After cortical lesions restricted to particular cytoarchitectonic areas, neurons in the sensory nuclei of the opossum thalamus appeared to be sustained by widespread collaterals which extended into the surrounding regions of cortex. Consequently, to produce severe degeneration in a thalamic nucleus it was necessary to make a large lesion which also included portions of the projection targets of adjacent nuclei. The opossum was contrasted in this study to more highly developed species such as the cat

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1. The following abbreviations are used in the Figures and text: AM, anteromedial nucleus; AV, anteroventral nucleus; GL, dorsal lateral geniculate body; GM, medial geniculate body; L, lateral nuclear group; LP, lateral posterior nucleus; MD, medial dorsal nucleus; Po, posterior group of nuclei; V, ventral nuclear group; VM, ventromedial nucleus; VP, ventral posterior nucleus; VGL, ventral lateral geniculate body.

in which thalamic regions are present which send essential projections to particular cortical areas. Thus small lesions confined to these areas in the cat produce a sharply localized region of severe degeneration in the corresponding thalamic nucleus.[2] On the basis of this difference between species the suggestion was made that precisely localized thalamo-cortical connections are a relatively recent accomplishment of mammalian evolution.

The first step in the present experiments was to conduct a similar investigation of thalamo-cortical relations on the hedgehog visual system. In many respects, the hedgehog appears to be an appropriate animal for testing the view that sustaining thalamo-cortical projections are a general characteristic of the visual system in primitive mammals. In terms of the relative expansion of new cortex to old, the hedgehog seems to have advanced in evolution even less than the opossum, and the lack of marked internal differentiation in either its cortex or thalamus supports the idea that this species has undergone relatively little change from ancestral mammals (Brodman, 1909; Erickson _et al_., 1967).

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2. The distinction between sustaining and essential projections was originally made by Rose and Woolsey (1958). These authors also suggested that the basis for sustaining projections may be neurons which by means of collaterals project to more than one cortical region.

In order to compare the hedgehog with the opossum, the anatomical experiments consisted of three parts. The purpose of the first two parts was to obtain a cytoarchitectonic analysis of the hedgehog visual cortex and lateral geniculate comparable to those which provided the basis for the study of thalamo-cortical connections in the opossum (Gray, 1924; Bodian, 1935; Diamond and Utley, 1963). The final part was concerned with the relations of the projections of the lateral geniculate to the cytoarchitectonically defined visual area.

The behavioral experiments on the hedgehog were conducted in conjunction with these anatomical studies. In general, the behavioral experiments were an effort to apply the results of the anatomical investigation to a study of the effects of cortical lesions on the ability to discriminate patterns. The primary concern was to determine if learned discriminations based on simple differences in pattern depend in the hedgehog on structural subdivisions defined in terms either of the projections of the lateral geniculate or of cortical cytoarchitecture. As in the anatomical experiments, at each point it was hoped that by study of the hedgehog, a basis could be obtained for interpreting from an evolutionary point of view the similarities and differences in cortical organization characteristic of the visual system in higher mammals.

ANATOMICAL METHODS

For purposes of studying the projections of the lateral geniculate by the method of thalamic retrograde degeneration, unilateral cortical lesions were made in fourteen hedgehogs. Two types of hedgehogs were used: an Egyptian variety, Hemiechinus auritus aegyptiacus and the common European genus, Erinaceous europaeus. Since no important differences were found between these species, the data obtained from the two will be combined. However, there are some minor differences and consequently in the following discussion the genus of each animal will be designated.

Surgical and Histological Procedures

The surgical procedures for all animals included in the retrograde degeneration study were similar. The animals were anesthetized with sodium pentobarbital at a concentration of 60 mg. per cc. An initial dose of 0.15 cc. of anesthetic was usually sufficient to produce a level of narcosis suitable

for prolonged surgery. In exceptional cases, an additional dose of 0.02 cc. was necessary.

The cortex was removed unilaterally by subdural aspiration under aseptic conditions. Following surgery, 0.1 cc. of antibiotic was administered.

After six weeks the animals were given a lethal dose of sodium pentobarbital and perfused with isotonic saline followed by 10% formalin. The brains were immediately removed from the skull and stored in formalin. After remaining in formalin for at least three to four days, the brains were photographed, then dehydrated, embedded in celloidin and cut transversely into sections 25 microns thick. An effort was made to section every brain in the same plane. Routinely, alternate sections through the thalamus and every tenth section through the remainder of the brain were stained with thionin. When it was necessary to study the nature of the lesion or the extent of thalamic degeneration in greater detail, additional sections were stained either by the Weil method or with thionin.

Reconstruction of the Lesions and Thalamic Degeneration

A surface view of the lesion was reconstructed by a dorsal projection of the transverse sections. To facilitate

comparisons between animals, the reconstructed lesion was then transferred to a standard dorsal view of the brain. The same procedure was used for both types of hedgehog, although slight differences in the shape and size of the brains necessitated the use of different standard dorsal views.

For most cases, the reconstructed lesion was transferred to the standard brain simply by correcting for individual differences in size. For each animal, however, the transfer to the standard was checked by comparing corresponding transverse sections through the experimental and standard brains for similarities in the appearance of subcortical structures. For example, a frontal section midway between the anterior and posterior boundaries of the visual cortex in an experimental animal should resemble in terms of the development of subcortical structures a similarly located section in the standard. For brains cut in the same plane the distance between the two frontals rarely exceeded 0.5 mm.

Generally, transverse sections through four levels of the visual cortex were drawn to illustrate the depth of the lesion. The lines through the dorsal views of the brains indicate both the level and the plane of these sections. Since the same four levels through the visual area were drawn

in all of the experimental brains, they are designated in the Figures by the letters A, B, C and D as well as by section numbers. In terms of the appearance of subcortical structures for example, sections A, B and C in Hedgehog 105 (Fig. 18, Page 57) can be seen to closely resemble the similarly labeled sections in Hedgehog 108 (Fig. 19, Page 59). Three rather than four transverse sections appear in the illustrations for these two cases since only sections within the boundaries of the lesion are presented. Occasionally, as in the case of Hedgehog 8 (Fig. 13, Page 47), the lesion extended considerably anterior to the boundary of the visual area. To provide a complete picture of the lesion an additional transverse section is presented. The additional sections are labeled only with a section number in the illustrations.

In anatomical cases with large lesions it was sometimes difficult to section each brain in exactly the same plane. In these cases, the dorsal view was drawn by transferring the lesion directly from the photographs to the standard brain. This could be accomplished with a high degree of accuracy since all photographs were taken from a dorsal perspective. Study of subcortical structures and the relation between the lesion as seen from the transverse and dorsal views provided an estimate of the actual plane of section.

To describe the thalamic degeneration, the region of the thalamus including the lateral geniculate was subdivided on the basis of morphological criteria into seven levels. Whenever possible, corresponding levels in different brains are presented in the Figures. The purpose of the matched thalamic sections once again was to facilitate comparisons between brains.

Illustration of Cortical and Thalamic Cytoarchitectonics

For the purpose of illustrating the cytoarchitecture of the hedgehog thalamus and cortex, photomicrographs were taken of transverse sections through a normal brain. The brain was cut at 50 microns instead of 25 microns and alternate sections through the cortex and thalamus stained by the Weil method and with thionin. In general, low power photomicrographs of 50 micron sections illustrate cortical and thalamic subdivisions more distinctly than the thinner 25 micron sections, while the latter are better suited for microscopic analysis of retrograde degeneration.

ANATOMICAL RESULTS

To provide a basis for analyzing the results of the retrograde degeneration experiments, it is necessary to describe first the cytoarchitecture of the posterior neocortex and lateral geniculate in the hedgehog. In the following section it will be shown that a visual area can be defined in this species and that, lateral to it, a band of cortex can be distinguished which separates the visual and auditory regions. The second section will describe the hedgehog lateral geniculate and surrounding thalamic nuclei. The projections of the lateral geniculate to the cortical regions defined in the first section will then be analyzed in the final part.

Cytoarchitecture of Visual Cortex

To compare the anatomical results obtained from the hedgehog with those reported for other species, it was essential to adopt corresponding cytoarchitectonic criteria

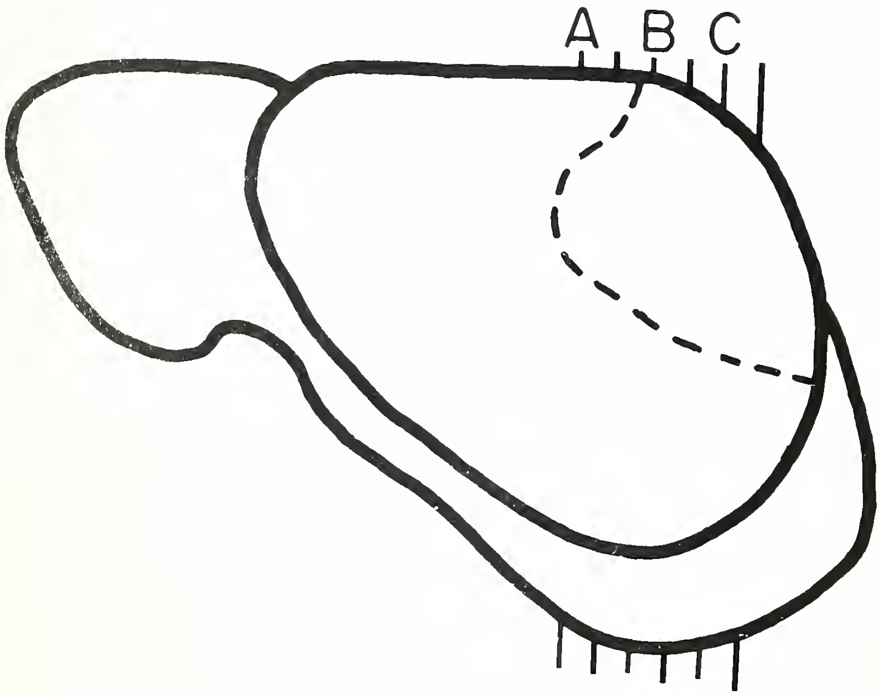
for mapping the visual area of neocortex. In the absence of a stripe of Gennari as distinct as that found in higher primates, the most common criteria for the visual area has been the relative thickness of layer IV. An increase in the thickness of the granular layer has provided the primary basis for defining visual cortex in species as divergent as the rat, rabbit, cat and opossum (Lashley, 1934b; Krieg, 1946; Rose and Malis, 1965; O'Leary, 1941; Gray, 1924) and, even more important, appears to correspond to a major projection target of the lateral geniculate (Lashley, 1934b; Rose and Malis, 1965; Sprague, 1965; Bodian, 1935; Diamond and Utley, 1963). Consequently, the same criterion was used in the following analysis of the hedgehog cortex. The descriptions of the visual cortex in other mammals, however, included mention of other cytoarchitectonic properties which are closely correlated with the thickness of layer IV. Some of these same features were also found in the hedgehog; in occasional sections they were used as additional landmarks when, due to characteristics of the stain or plane of cut, layer IV appeared inadequate for precise determination of a particular boundary. It is important to emphasize, however, that if the data from all the brains studied are taken into consideration, the same results can be obtained on the basis of changes in layer IV alone.

Figure 2 shows the position of the transverse sections chosen to illustrate the extent of visual cortex in the hedgehog. The three sections designated by letters are at the same level through the visual area as the sections used to illustrate the extent of the cortical lesions in experimental brains.

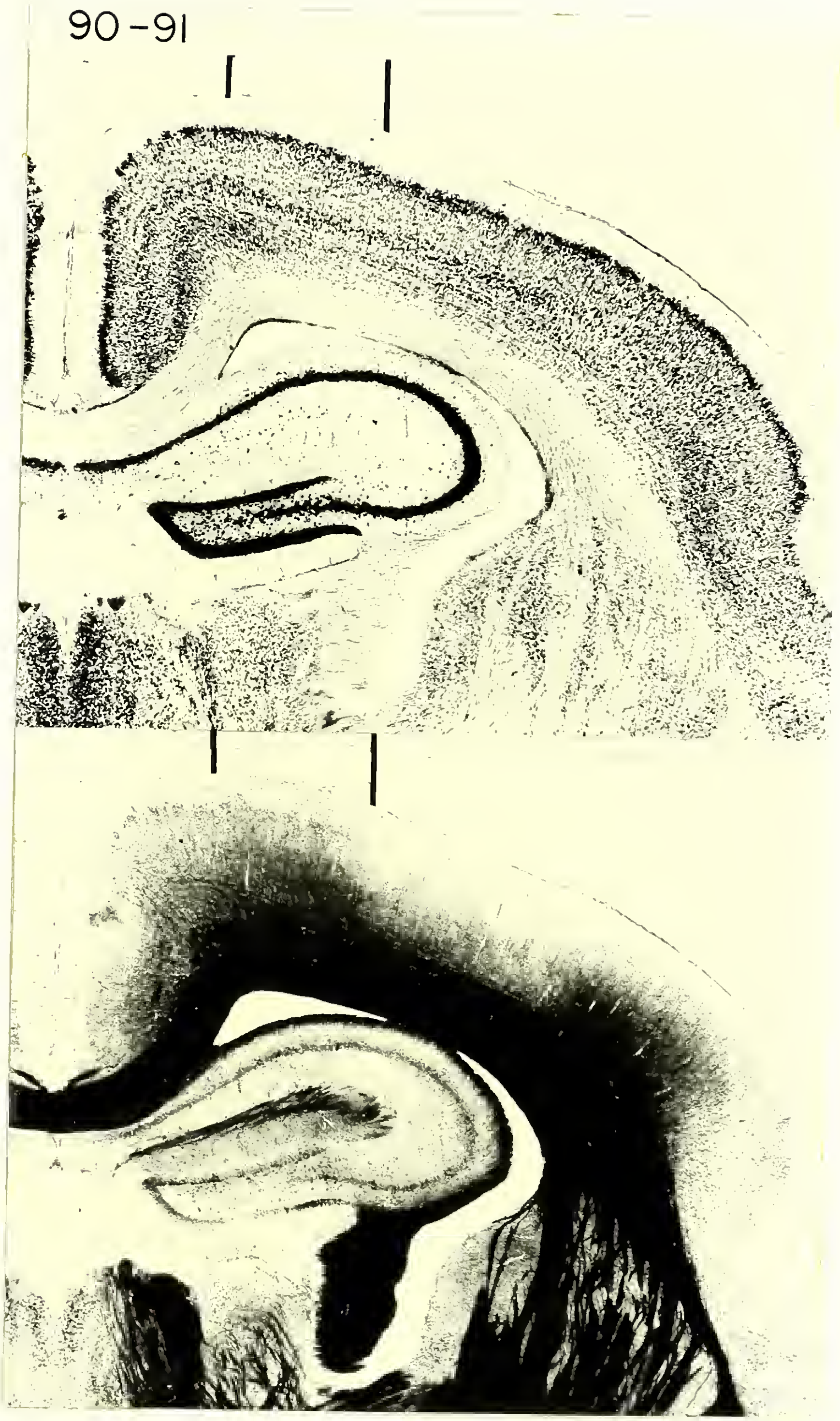
Figures 3 to 8 are photomicrographs of adjacent sections at each of these positions. The upper section was stained with thionin for the cell bodies and the lower by the Weil technique to reveal the fibers. The vertical lines on the photomicrographs mark the boundaries of the visual area. Since the midlines of the adjacent sections are aligned on the Figure, the vertical lines also indicate the correspondence between the boundaries revealed by the two stains.

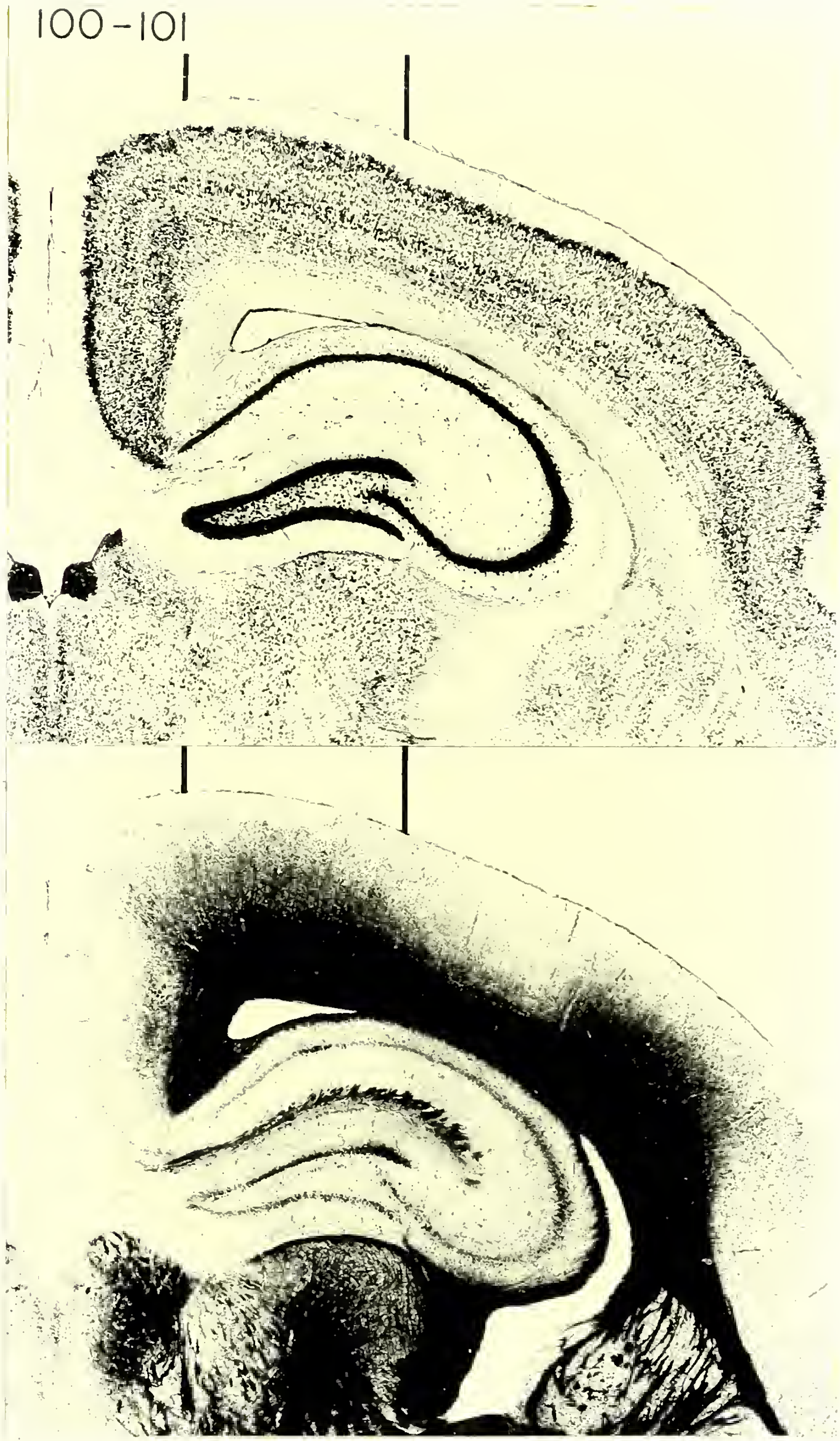
Sections 90 and 91 are located near the anterior tip of the visual area and correspond to level A in experimental brains. In the thionin stained preparation, the primary feature which distinguishes the visual area from surrounding cortex is the slight increase in the thickness of layer IV. The lateral border of visual cortex is marked by a slight downward slope of layer II. Layer I resembles the homologous layer in all mammals and requires little comment, except perhaps to note that it is relatively thick in the hedgehog. Layer II is thin and consists primarily in clumps of small

Figure 2. Dorsal View of Hedgehog Neocortex. The vertical lines indicate the locus of the frontal sections photographed to illustrate the cytoarchitecture of the posterior neocortex. The dashed line indicates the boundaries of the visual area as defined by cytoarchitecture.

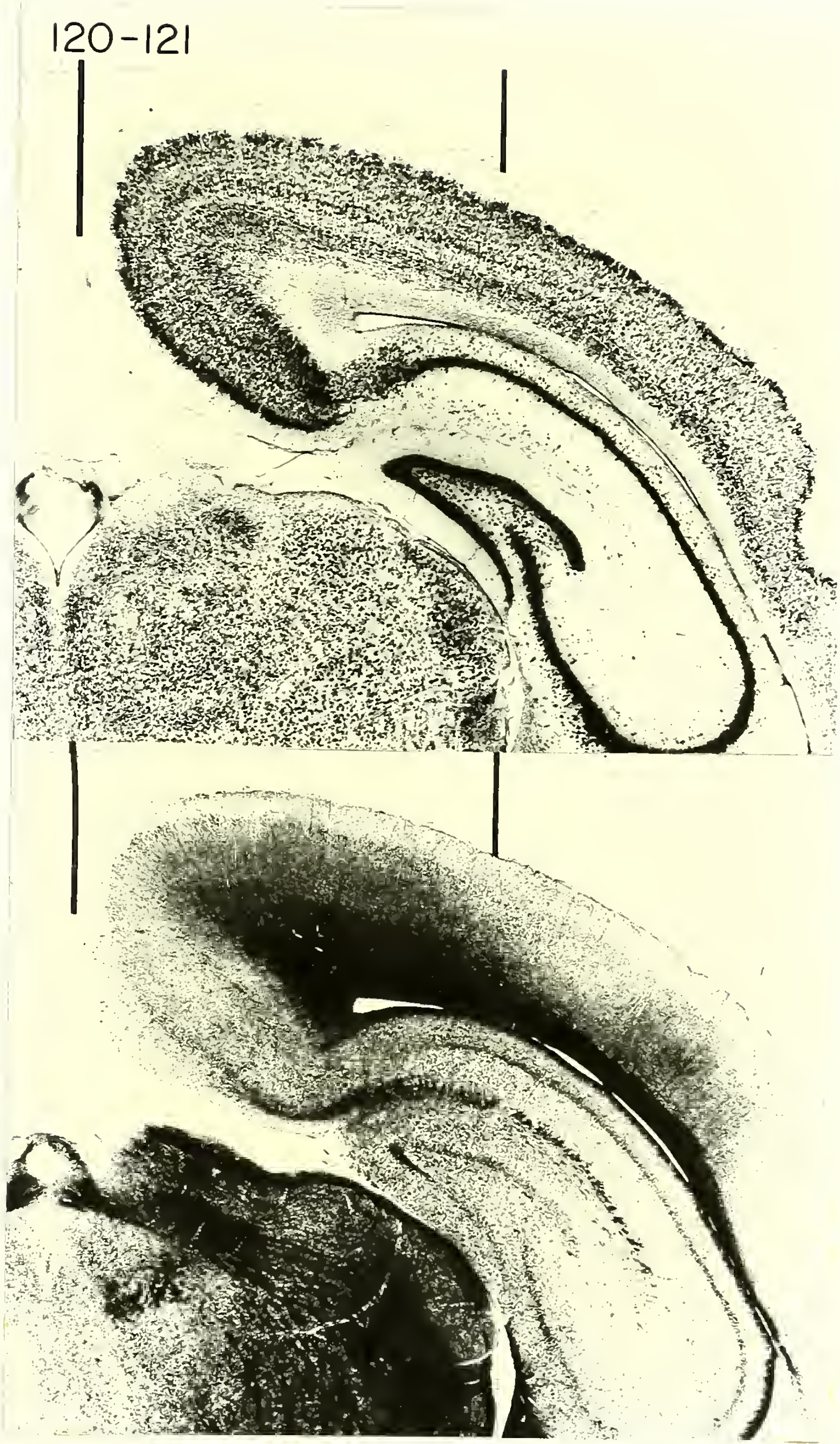

A
B
C

Figures 3-8. Photomicrographs of the Posterior Neocortex in the Hedgehog. The upper section in each Figure is stained with thionin, the lower by the Weil technique. The lines on the photomicrographs are intended to indicate the correspondence between the boundaries of the visual area revealed by the two stains.

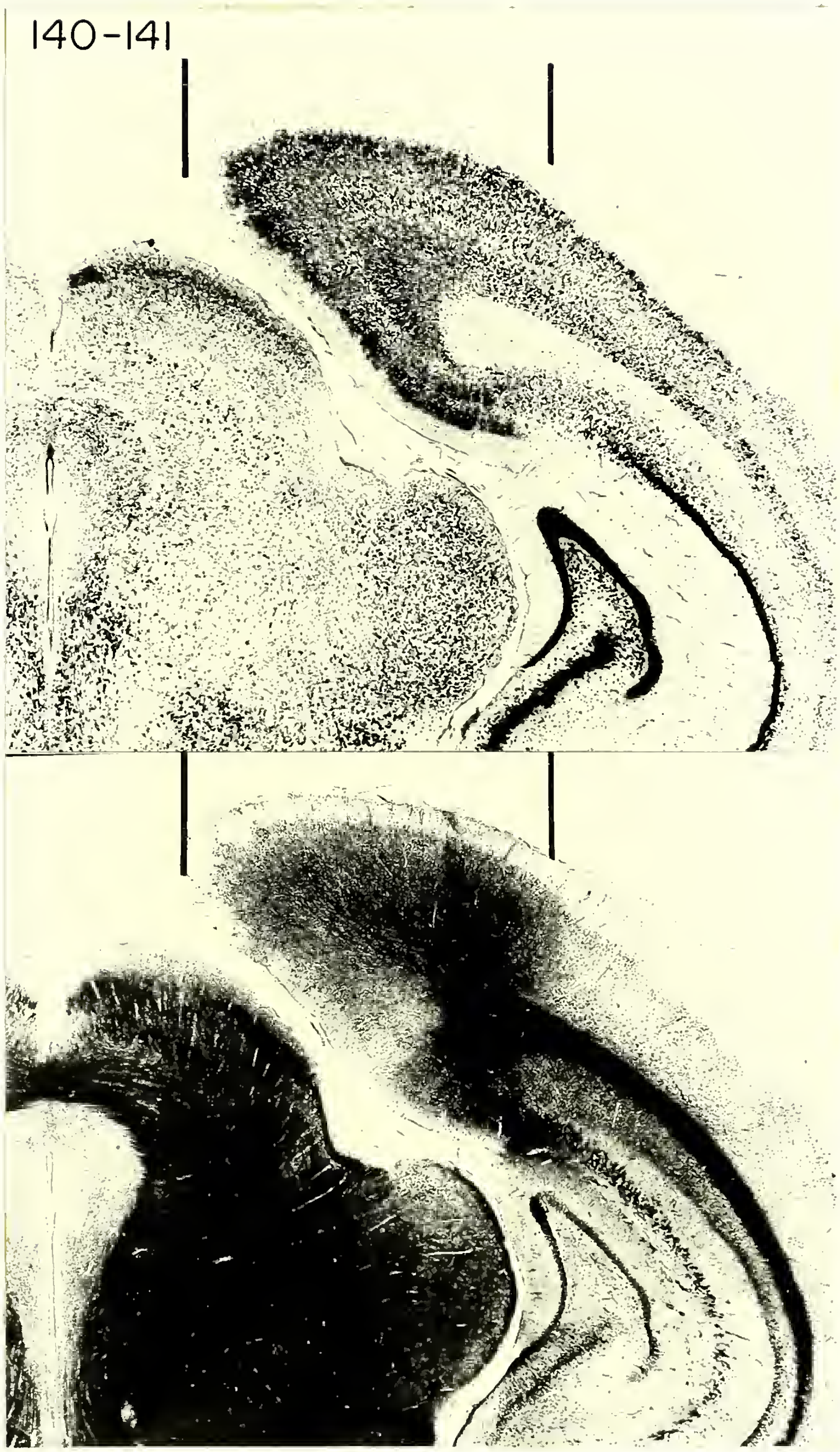

90-91


100-101


110-111


120-121


130-131


140-141

pyramidal shaped cells. Layer III either is not present at this level or is fused with layer II, a condition also found in the rat and the rabbit (Krieg, 1946; Rose and Malis, 1965). Layer IV is relatively thick and consists primarily of a homogeneous population of medium sized granular cells. The visual area also exhibits a prominent layer V consisting of medium sized pyramidal cells which form a layer four to five cells thick. The dark staining properties of these neurons provide a relatively sharp contrast between this layer and layers IV and VI. Layer VI in the hedgehog resembles the corresponding layer described in other mammals. The decrease in density of its neurons in the visual area provides another consistent landmark which is also found in the rat (Krieg, 1946).

In the fiber stained sections the visual area can be distinguished by the dense plexus of fibers which begins in layer VI and ends rather abruptly at the external boundary of layer IV. On either side of the visual area the cortex is characterized by a less dense network of fibers which, further laterally, terminates at a second dense plexus. This lateral region of dense fibers probably corresponds to primary auditory cortex. Between the auditory area and the rhinal sulcus lies a region of cortex almost devoid of stained fibers.

By sections 100 and 101, the visual area has expanded both medially and laterally. Once again the increased thickness of layer IV is the main distinguishing feature in the thionin stained section. Laterally, the boundary is still demarcated by an inward slope of layer II. Medially, layer IV narrows more gradually than in the previous section. The decreased density of cells in layer VI, however, still provides a distinct landmark. In the fiber stained section the contrast between visual cortex and the area lateral to it is even sharper than in the previous section due to a further decrease in the density of fibers in the lateral region. Auditory cortex can still be seen further laterally and between it and the rhinal sulcus, the second "afibrous" region. The auditory region appears to differ from the visual area primarily by a denser network of fibers and, in the thionin preparation, the absence of a distinct layer V.

Sections 110 and 111 correspond to level B in experimental brains. The visual area is still expanding both medially and laterally. Although layer IV narrows gradually toward the midline, on the basis of the concentrations of neurons in layer VI and the density of fibers in the section stained by the Weil technique, it appears to extend almost to the midline. The fibers in the region lateral to visual cortex have almost entirely disappeared

at this level and in the thionin preparation layer V in this region is also less distinct. The number of fibers in auditory cortex has also decreased so that this region is now less prominent than the visual area.

At sections 120 and 121, the medial wall of the cortex has begun to move away from the midline. Although layer IV of visual cortex still appears to narrow gradually toward the midline, the fiber preparation and the appearance of layer VI in the cell stain indicate that it now extends to the medial wall. The characteristic afibrous region is still situated lateral to the visual area and, lateral to it, the auditory region has almost disappeared.

At about the depth of layer V in the fiber stain, a light stripe running from medial to lateral through visual cortex can be detected separating the fiber concentrations in layers VI and IV. The network of fibers in layer IV may be homologous to the stripe of Gennari in higher primates. The darker plexus of layer VI probably corresponds to the inner stripe of Baillarger of classical cytoarchitectonics.

Sections 130 and 131 correspond to level C. The auditory cortex has now completely disappeared, leaving only the afibrous region lateral to visual cortex. In the cell stain, this afibrous area becomes more undifferentiated as it proceeds laterally, and near the rhinal sulcus exhibits

only four distinct layers. The light stripe can still be seen running parallel to the surface of the cortex through the visual area.

By sections 140 and 141 only two types of cortex remain on the lateral surface. Medially, the visual area is still prominent, extending from the midline approximately half the distance to the rhinal sulcus. Lateral to the visual area, there is only undifferentiated cortex as far as the rhinal sulcus. Essentially the same organization of the cortex persists to the posterior tip of the hemisphere.

The Organization of the Hedgehog Thalamus

Since the neuroanatomy of the hedgehog is not well documented in comparison to more common experimental mammals, and since many of the thalamic nuclei which in more highly developed animals are clearly differentiated often appear without distinct boundaries in this species, it is important to illustrate with photomicrographs the basis for our analysis of the thalamus. The chief justification, however, lies in the fact that the hedgehog thalamus may closely approximate the level of development attained by the actual common ancestors of mammals.

For illustrating the thalamus nine photomicrographs

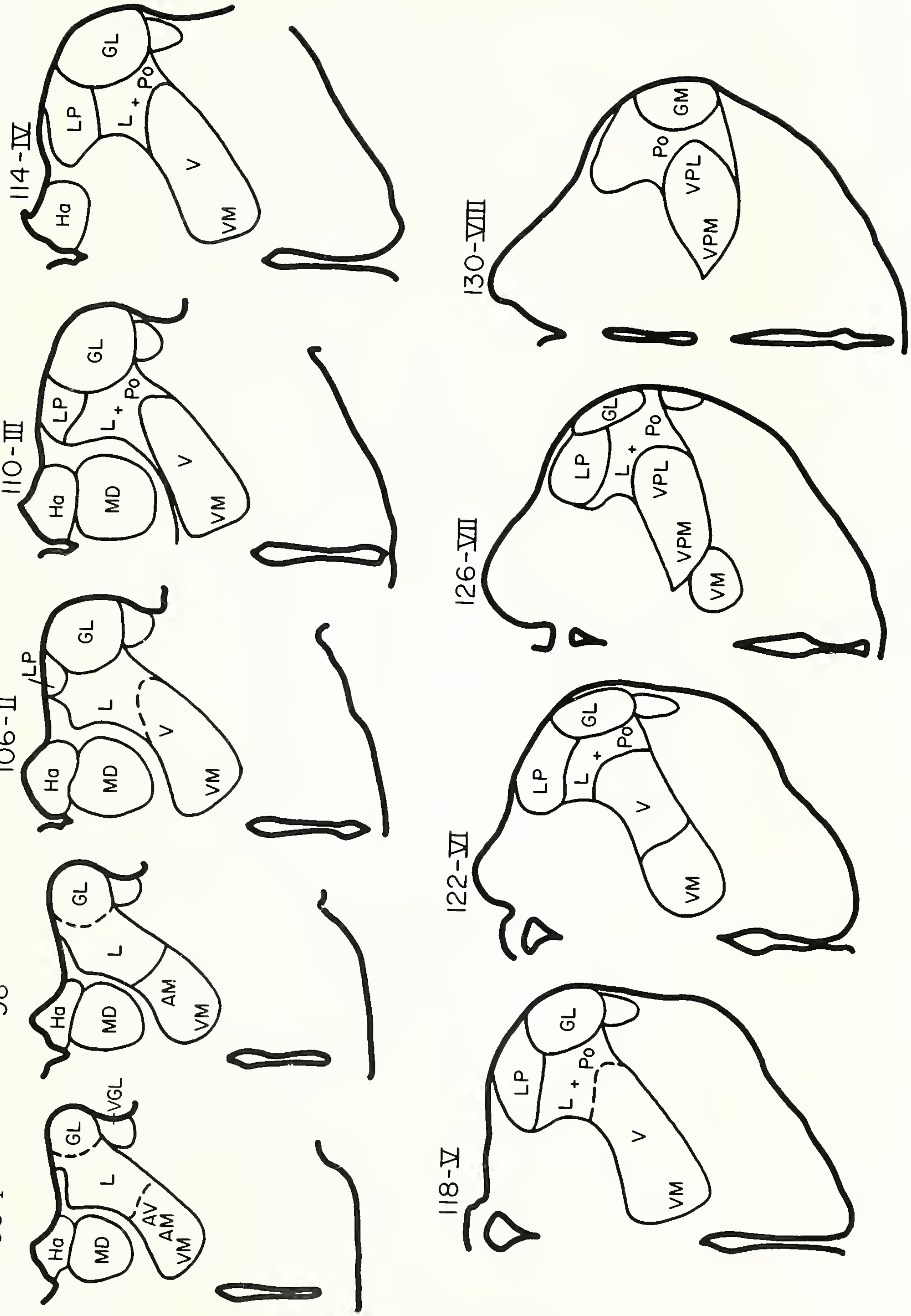
(Figs. 10 to 12) were chosen, eight of which closely represent the thalamic levels drawn to illustrate the retrograde degeneration in experimental animals. Figure 9 is a series of drawings of the photomicrographs showing the interpretation which was made of the various nuclear groups.

Section 96 includes the thalamus near the anterior boundary of the lateral geniculate (GL). When GL first emerges it appears to be almost continuous with the adjacent sector of the lateral nuclear group (L). The cell size, shape and depth of stain is very similar in these two nuclei. A boundary between the two is suggested, however, by the slight differences in the concentration and arrangement of their respective neurons. This boundary is indicated in the drawing by a broken line. The lateral nuclei appear to extend from the anterior thalamus to the posterior levels of GL and consequently have been designated by the generic term "lateral group" or simply "lateral nucleus."

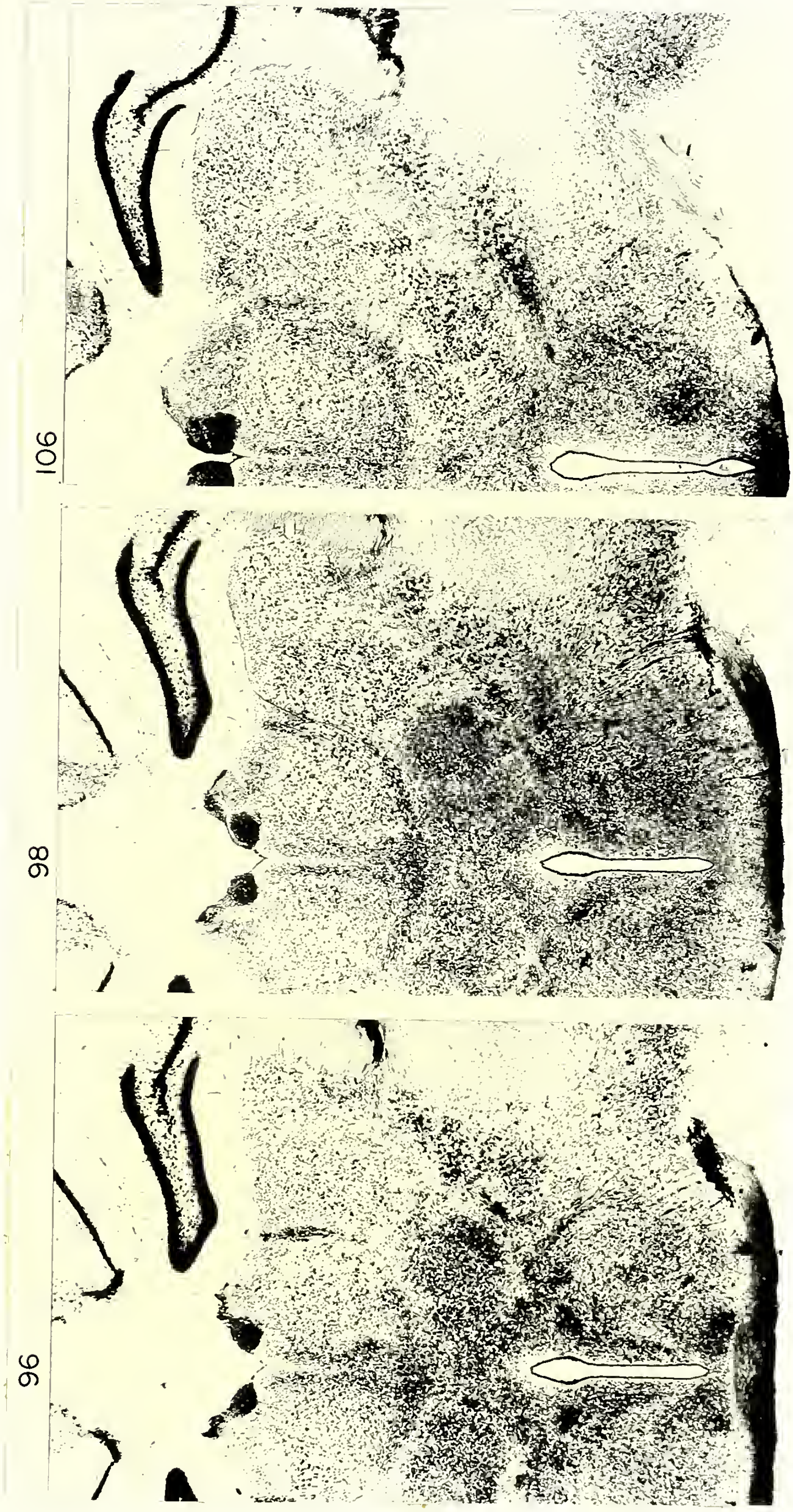
The anterior nuclear group is divisible at this level into two portions, the anteromedial (AM) and the anteroventral (AV) nuclei. The anterodorsal nucleus which is characteristic of most if not all experimental mammalian species is not apparent in the hedgehog, an observation first noted by Le Gros Clark (1929). Medial to and almost continuous with AM is the ventromedial nucleus (VM) of the ventral group.

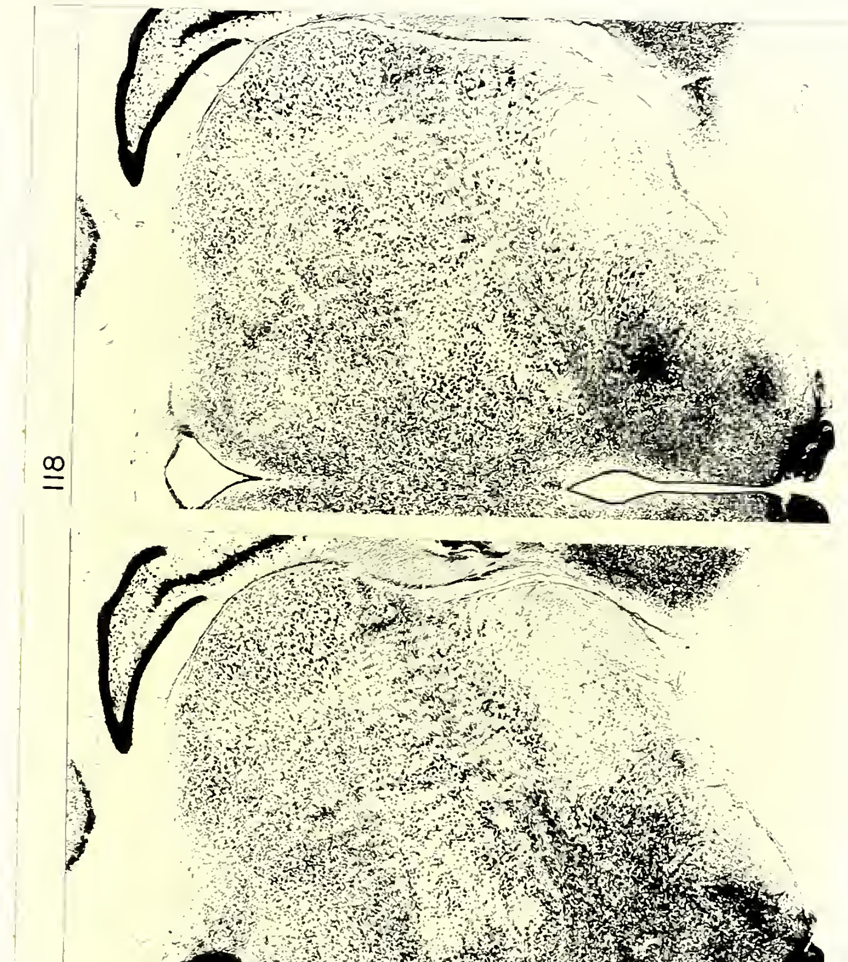
Figure 9. Drawings of the Hedgehog Thalamus. The drawings are an interpretation made of the photomicrographs presented in Figures 10-12.

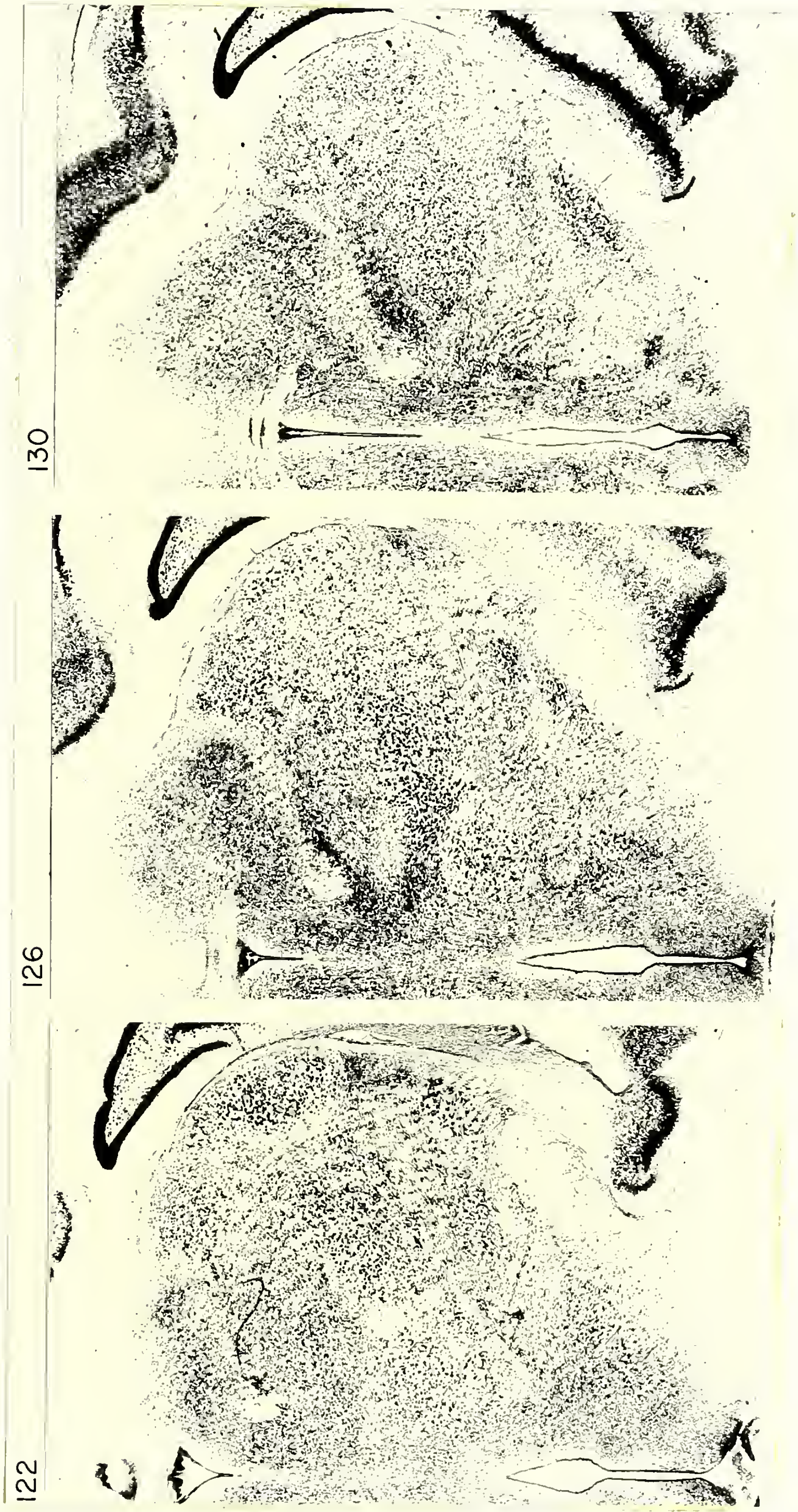
HEDGEHOG 97 (Egyptian)



Figures 10-12. Photomicrographs of the Hedgehog Thalamus. Each section was cut at 50 microns and stained with thionin. The photomicrographs are intended to show the cytoarchitectonic relations between GL and surrounding thalamic nuclei.


106
98
96


118
114
110


130
126
122

Two sections posteriorly (section 98), the division between L and GL is more distinct, primarily because of a thin strip of fibers located at their most ventral border. Dorsally, the two nuclei still appear almost continuous. AV has disappeared at this level, being replaced by the ventral extension of L.

By section 106, the fibrous region separating L and GL is more extensive; consequently the distinction between these two nuclei is quite definite. The few neurons which remain scattered among the fibers have been included in L. More posteriorly, L will fade without boundary into the posterior nucleus (Po). Medial and dorsal to GL a small subdivision of L can be defined which appears to be homologous to the lateral posterior nucleus (LP) of common experimental mammals such as the rat.

The anterior nuclei at this level have been completely replaced by the ventral nucleus (V). Since no further subdivisions could be made in this region until the emergence caudally of the ventral posterior nucleus (VP), the term ventral nucleus was used.

Proceeding posteriorly (section 110), LP and GL expand in size while L remains relatively stable. Although the boundaries between LP and GL on one hand and L on the other hand become more distinct, the border between LP and GL is

marked only by a slight band of decreased cell concentration.

The size of LP has increased considerably in section 114 and can be distinguished from GL by the more scattered distribution of its neurons. L at this level has been reduced primarily to a small wedge of neurons between LP and the dorsomedial tip of V. Intercalated between GL, V and L is a transition zone consisting of fibers and scattered neurons. In accordance with an earlier description of the hedgehog posterior thalamus, this region is called Po (Erickson et al., 1967).

In sections 118 and 122, GL decreases in size while LP remains relatively stable. A small segment of L remains, fading gradually into Po.

Section 126 is near the posterior tip of GL. The ventral nucleus has now assumed the "teardrop" shape characteristic of VP in other mammals (Erickson et al., 1967). VM can be seen as a small circle of cells just ventral to the medial sector of VP. Within VP, a further subdivision is apparent which probably corresponds to VPM and VPL of higher mammals. LP is still prominent at this level, whereas L has almost disappeared.

The posterior thalamus at the level of the medial geniculate (GM) is shown in section 130. Both GL and L have completely disappeared leaving only GM, VP and an inter-

calated zone of cells which has been designated as Po (Erickson et al., 1967). Note that the dorsal portion of Po occupies the same position relative to GM which LP holds relative to GL in more anterior sections.

The Cortical Projection of the Lateral Geniculate

One of the chief findings from the study of thalamo-cortical connections concerned the relations between the size of cortical lesions and the severity of the resulting degenerative changes in the thalamus. Severely degenerated zones are almost completely devoid of neurons. Only with a higher power (250X) of the microscope could an occasional shrunken neuron be detected. These severely affected cells were hardly larger than the surrounding glia. In severely degenerated regions even these small ghosts were rare and always apparently randomly distributed. In the illustrations, severe degeneration is indicated by black.

At the other extreme, in regions of slight degeneration, the affected neurons appear almost normal in size and color under low power magnification (60X) of the microscope. Closer observation with higher power, however, reveals minimal cell changes together with slight gliosis, in the absence of obvious cell loss. Regions of slight degeneration are indicated by

widely spaced dots in the Figures.

Obviously, moderate degeneration lies between the two extremes just described. In a typical instance of moderate degeneration many neurons remain in the degenerated zone but all show distinct retrograde changes. The moderately degenerated zones are depicted by closely spaced dots in the Figures.

The topographic projection of GL to visual cortex. The fact that GL projects topographically to visual cortex is evident from the degeneration produced by partial removals of this region. Cases 8, 55, 105, 108 and 112 all have lesions which removed anterior visual cortex but spared varying amounts of the posterior pole (Figs. 13, 15, 18, 19, 20, Pages 47, 51, 57, 59, 61). In each case, the resulting thalamic degeneration is most severe in posterior GL. The lesion in Case 58 on the other hand, spared anterior visual cortex; correspondingly, the degeneration is the least severe in posterior GL (Fig. 16, Page 53). The projection of GL to the medial portion of the visual area is apparent in Cases 105, 108 and 112 (Figs. 18, 19, 20, Pages 57, 59, 61). In each animal the lesion continues more posteriorly near the midline than at the lateral border of visual cortex and the degeneration is most severe in the ventral half of anterior GL.

<u>The effects of small visual cortex lesions</u>. In spite of the topographic relations revealed by subtotal removal of the visual area, the projections of GL neurons appear to be widespread. Small lesions of the size which would result in a restricted locus of severe degeneration in higher mammals produce only slight degeneration in GL of the hedgehog. Figure 21 (Page 63) is a summary of the lesions made which resulted in only slight changes in GL neurons. In many of the smallest cases, the changes were so subtle that often it was difficult to distinguish with certainty degeneration from normal variations which are often found in the appearance and distribution of neurons in GL. Figures 22 and 23 (Pages 65 and 67) present the details of the cortical ablation and thalamic degeneration for the largest two of these lesions. Although large proportions of GL are affected, in neither case was the degeneration ever more than slight.

<u>The effects of large visual cortex lesions</u>. The conclusion that the neurons only slightly affected by the small lesions are sustained in part by widespread projections within the visual area is suggested by the fact that as the size of the lesion is increased to include the regions removed by two or more of the smaller cases, the degeneration becomes more severe (Figs. 13, 15, 18, 19, 20, Pages 47, 51, 57, 59, 61). Following lesions that take out at least 50% of the

visual area, essentially the entire lateral geniculate is affected; yet no portion of the nucleus exhibits more than moderate degeneration. The widespread nature of the degeneration following partial visual cortex lesions, combined with the fact that the degeneration is not severe, suggests that individual GL neurons project diffusely. This conclusion depends, of course, on the assumption that collaterals of axons are sustaining the cell body.

The effects of lesions extending beyond visual cortex. Even the lesions in Cases 8, 105 and 108 which include almost all of the visual cortex do not produce severe degeneration, suggesting that GL may also project beyond the boundaries of the visual area (Figs. 13, 18, 19, Pages 47, 57, 59). Severe degeneration in GL is found only after very large lesions which extend considerably beyond the borders of visual cortex, or after lesions which damage underlying fibers (Figs. 14, 15, 16, Pages 49, 51, 53). For example, in Case 58 (Fig. 16, Page 53) the lesion destroyed all of the cortex both medial and lateral to the posterior levels of the visual area, and the anterior half of GL is severely degenerated.

That the projections of GL outside the boundaries of visual cortex are sustaining in nature is further suggested by Case 61 which is a moderate size lesion restricted primarily

to the region lateral to the visual area (Fig. 17, Page 55). Although degeneration is found throughout GL, due perhaps to partial damage of the underlying fibers, the retrograde changes are never more than slight. Severe degeneration in GL would appear to depend on a lesion that includes several cortical regions, each of which taken out alone produces only slight or moderate degeneration.

The cortical projections of the lateral nuclei. Since the majority of lesions made in the present study were confined primarily to visual cortex, it is impossible to describe with confidence the projections of the lateral nuclei, L and LP. In addition, each of these nuclei is permeated with fibers many of which apparently are the cortical radiations of the lateral geniculate. Consequently, lesions confined to the visual area may produce gliosis in L and LP due to fiber degeneration which closely resembles the slight degeneration produced in GL after small ablations.

Several of the lesions do, however, indicate that these nuclei project primarily to cortex surrounding the visual area. The ablation in Case 105, for example, was confined primarily to the visual area and little or no degeneration was present in either L or LP (Fig. 18, Page 57). The lesion in Hedgehog 108 on the other hand was similar to

105 except that it extended medially to include most of the medial wall adjacent to the visual area (Figs. 19, 18, Pages 59, 57). The severity of degeneration in L was increased to moderate whereas LP still exhibited little or no degeneration. The lesion in Hedgehog 112 also removed the medial wall but included more cortex anterior and medial to the visual area (Fig. 20, Page 61). The degeneration in L is moderate or severe whereas LP is still for the most part unaffected. Evidently, L projects primarily to the medial wall adjacent and anterior to the visual area. At the same time, even the lesions in Cases 8 and 112 produced only moderate degeneration in L suggesting that the total projection target of this nucleus may be much more widespread (Figs. 13, 20, Pages 47, 61). The large lesion in Case 58 spared a portion of the cortex anterior and medial to the visual area; although the degeneration extends throughout L, it is still never more than moderate (Fig. 16, Page 53). It would be necessary to make a larger lesion which includes this anteromedial cortex in order to determine with certainty whether a cortical lesion can produce severe degeneration in L. Larger lesions made in the behavioral experiments, however, suggest that this is the case (e.g., Figs. 47-48, Pages 126, 127).

LP, on the other hand, appears to project primarily to cortex lateral to the visual area. Thus the lesions in

Cases 8, 105 and 112 were confined to cortex in and medial to the visual area and little or no degeneration was present in LP (Figs. 13, 18, 20, Pages 47, 57, 61). The lesion in Hedgehog 25 extended lateral to the visual area and the degeneration in a large proportion of LP was increased to moderate (Fig. 14, Page 49). In Hedgehog 58 most of the visual area and in addition, the cortex laterally as far as the rhinal sulcus was removed (Fig. 16, Page 53). The degeneration in LP was severe. The lesion in Case 61, on the other hand, is confined primarily to the lateral cortex and the degeneration in LP is only slight, suggesting that, like GL and L, this nucleus projects in a sustaining manner to extensive cortical regions (Fig. 17, Page 55).

The pattern of retrograde degeneration in the thalamus of Hedgehog 58 also suggests that topographically, the projection of LP corresponds to that of GL (Fig. 16, Page 53). Thus the severe degeneration in LP was confined to the anterior thalamic levels which also exhibited severe degeneration in GL. Posteriorly both GL and LP are only moderately degenerated.

Figure 13. Cortical Lesion and Thalamic Degeneration in Hedgehog 8. Although the lesion removes a major portion of the visual area, the degeneration in GL is never more than moderate. The slight degeneration in Level I of GL reflects the spared portion of posterior visual cortex. The slight degeneration in dorsal GL in Levels III and IV corresponds to the spared visual cortex along the lateral border.

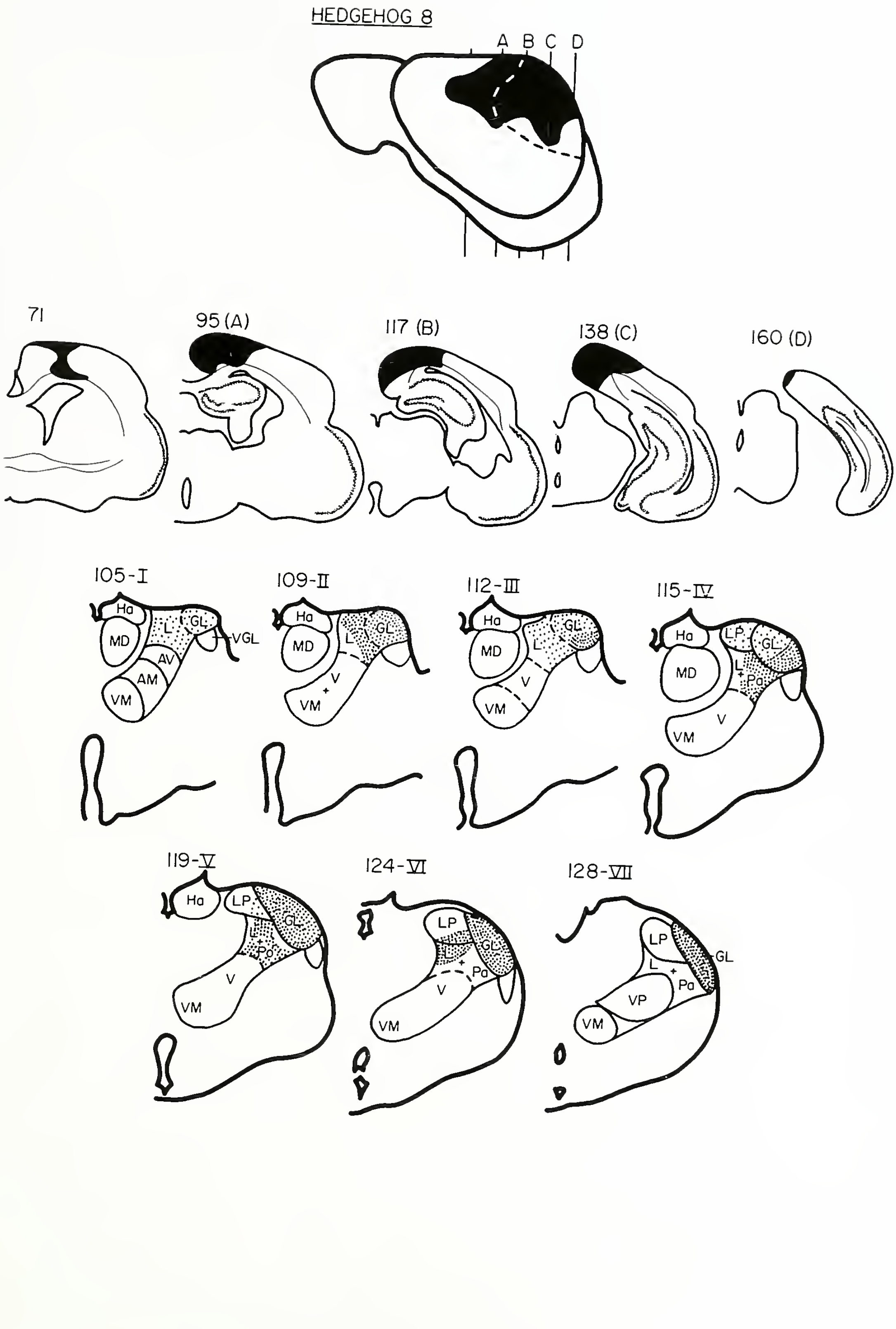

HEDGEHOG 8
A B C D
71
95 (A)
117 (B)
138 (C)
160 (D)
105-I
Ha
MD
L
GL
VGL
AV
AM
VM
109-II
112-III
115-IV
LP
Pa
V
119-V
124-VI
128-VII
VP

Figure 14. Cortical Lesion and Thalamic Degeneration in Hedgehog 25. This brain is included primarily to show that extension of a cortical lesion to include lateral regions in addition to the visual area results in moderate degeneration in LP. Cases 8 and 112 for example, spared this lateral region and LP is less severely degenerated (Figs. 13, 20, Pages 47, 61).

HEDGEHOG 25 (European)

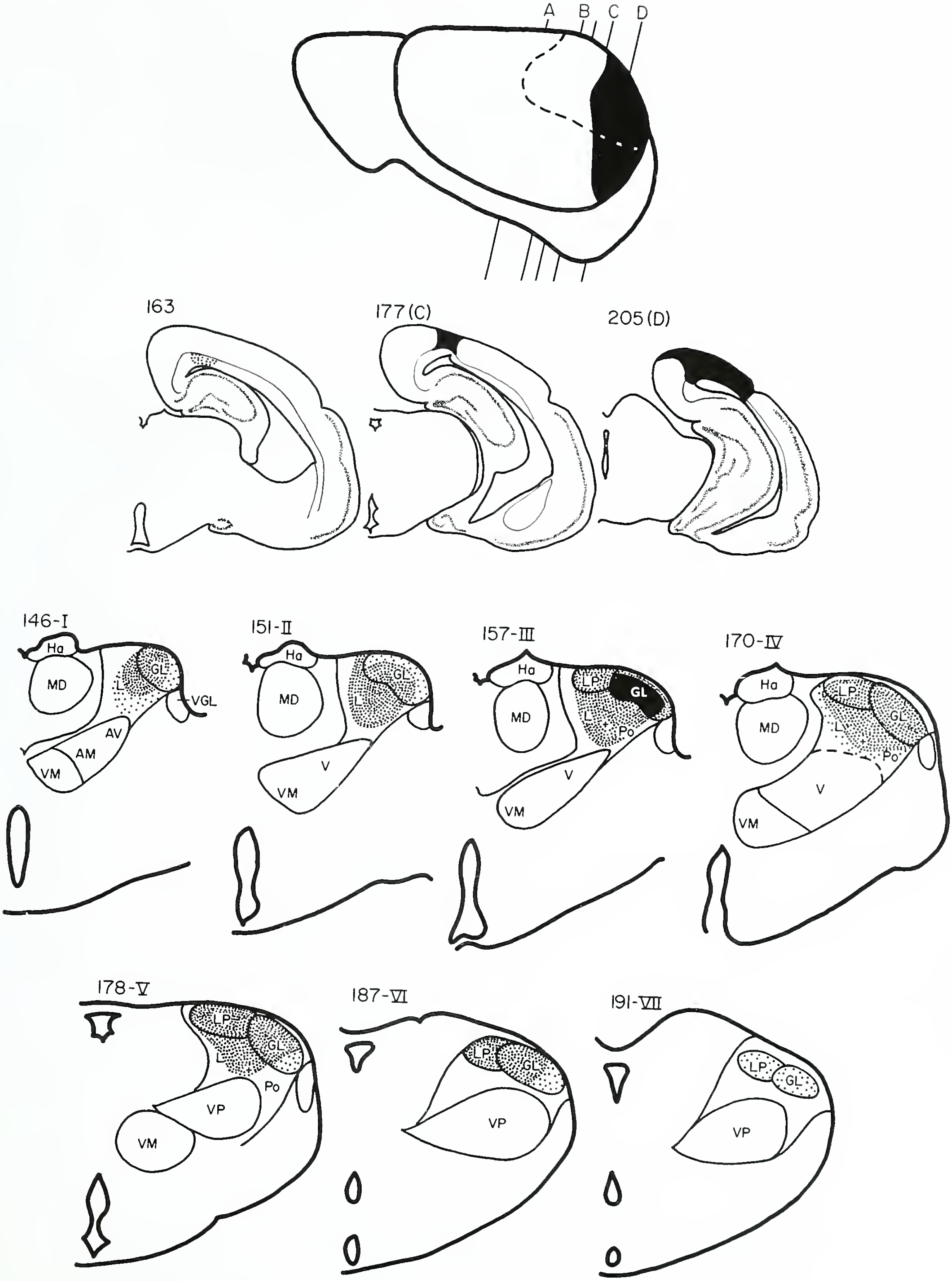
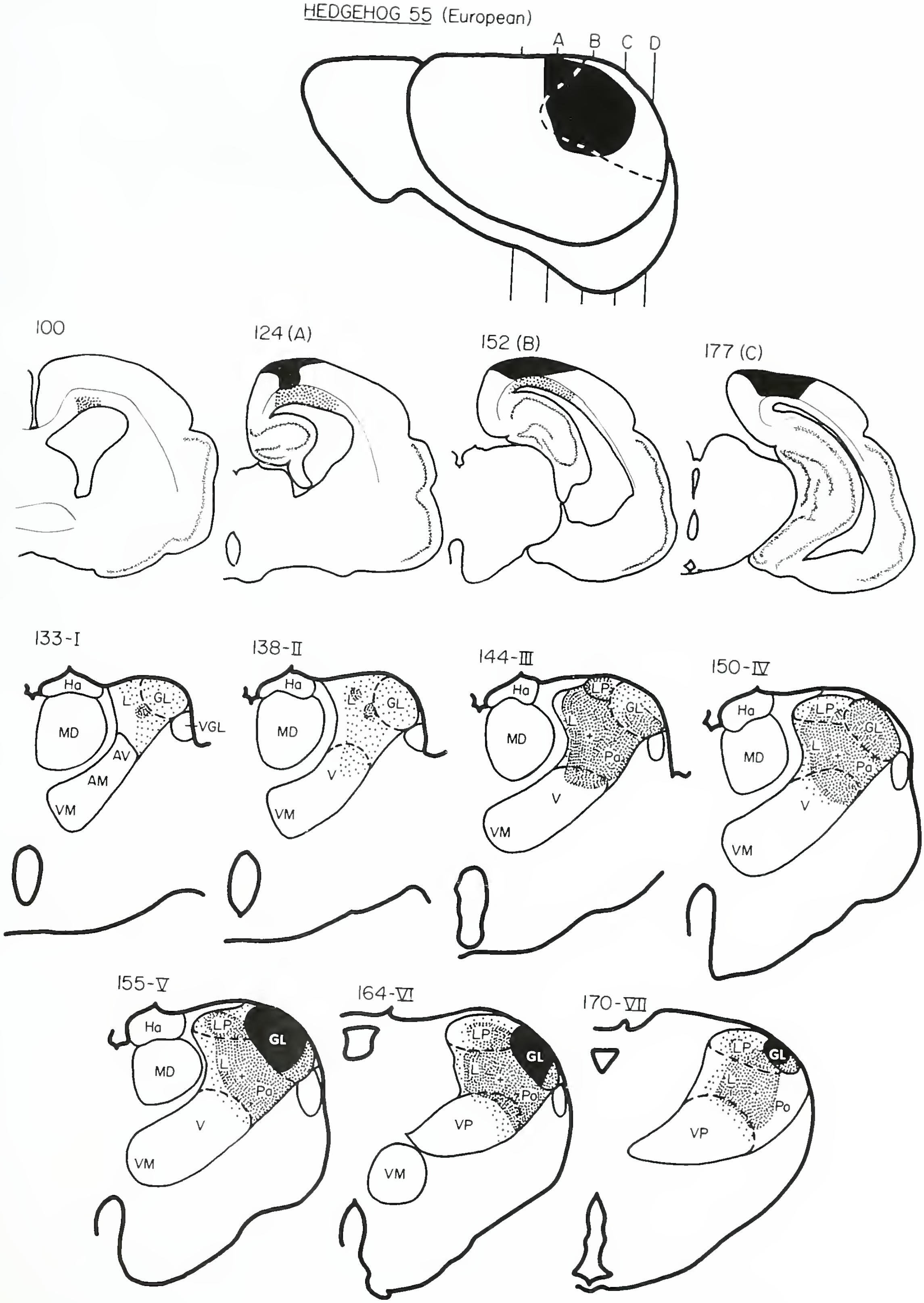


Figure 15. Cortical Lesion and Thalamic Degeneration in Hedgehog 55. This is a large lesion confined primarily to anterior visual cortex. As a result of sparing posterior visual cortex, anterior GL is only slightly affected. The severe degeneration in portions of posterior GL may reflect the damage to the fibers underlying anterior visual cortex which project to regions medial and lateral to this area.



HEDGEHOG 55 (European)
A
B
C
D
100
124 (A)
152 (B)
177 (C)
133-I
Ha
MD
L
GL
VGL
AV
AM
VM
138-II
Ha
MD
L
GL
V
VM
144-III
Ha
MD
LP
GL
L
Pa
V
VM
150-IV
Ha
MD
LP
GL
L
Pa
V
VM
155-V
Ha
MD
LP
GL
L
Po
V
VM
164-VI
LP
GL
L
Po
VP
VM
170-VII
LP
GL
L
Po
VP

Figure 16. Cortical Lesion and Thalamic Degeneration in Hedgehog 58. This is a large lesion which includes all of the cortex medial and lateral to the posterior portion of the visual area. Anterior GL and LP are severely degenerated. The moderate degeneration in posterior GL corresponds to the spared anterior segment of visual cortex.

HEDGEHOG 58 (European)

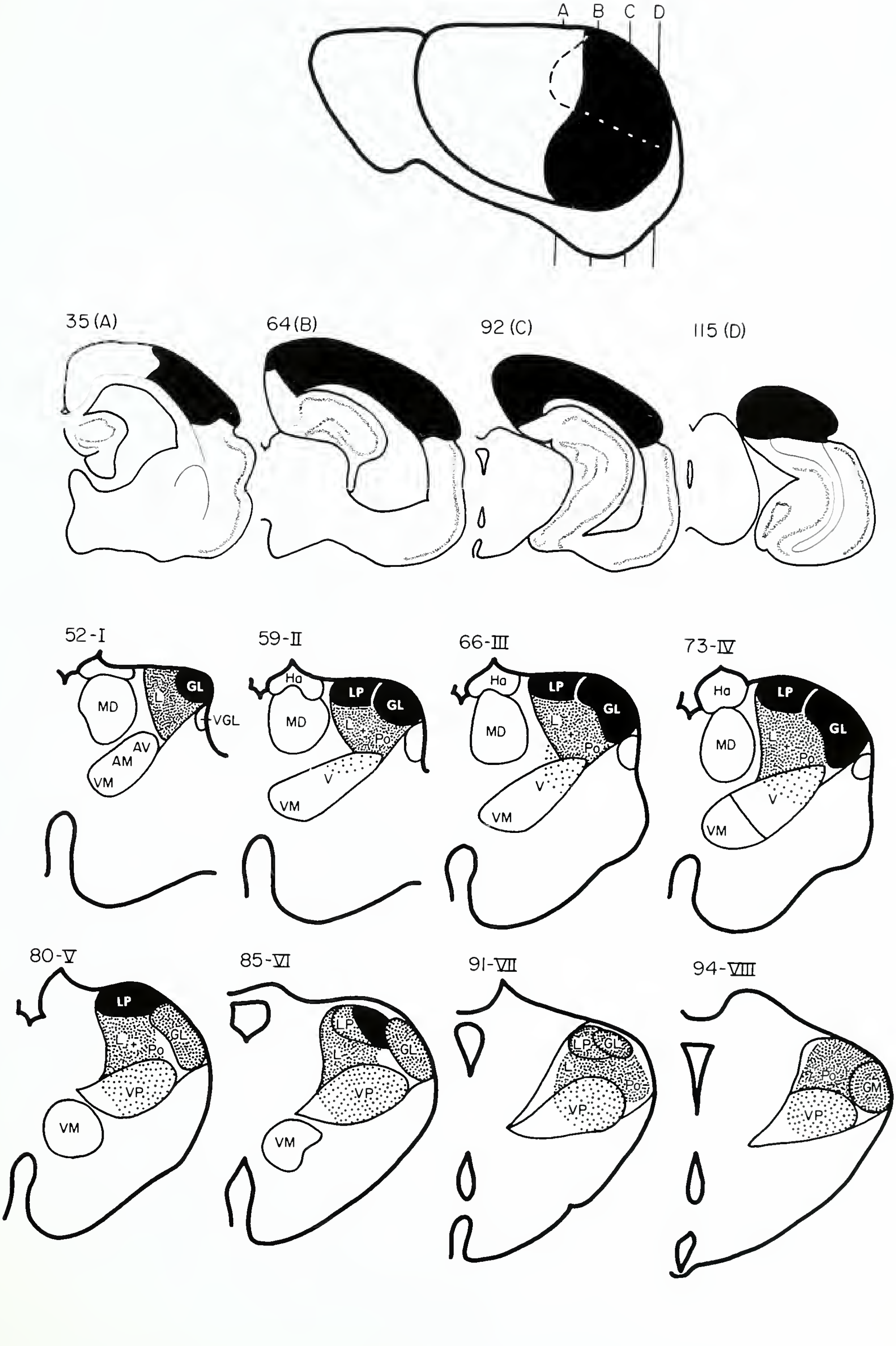


Figure 17. Cortical Lesion and Thalamic Degeneration in Hedgehog 61. The lesion is confined primarily to cortex lateral to the visual area. Although degeneration is found throughout GL, the changes are never more than slight.

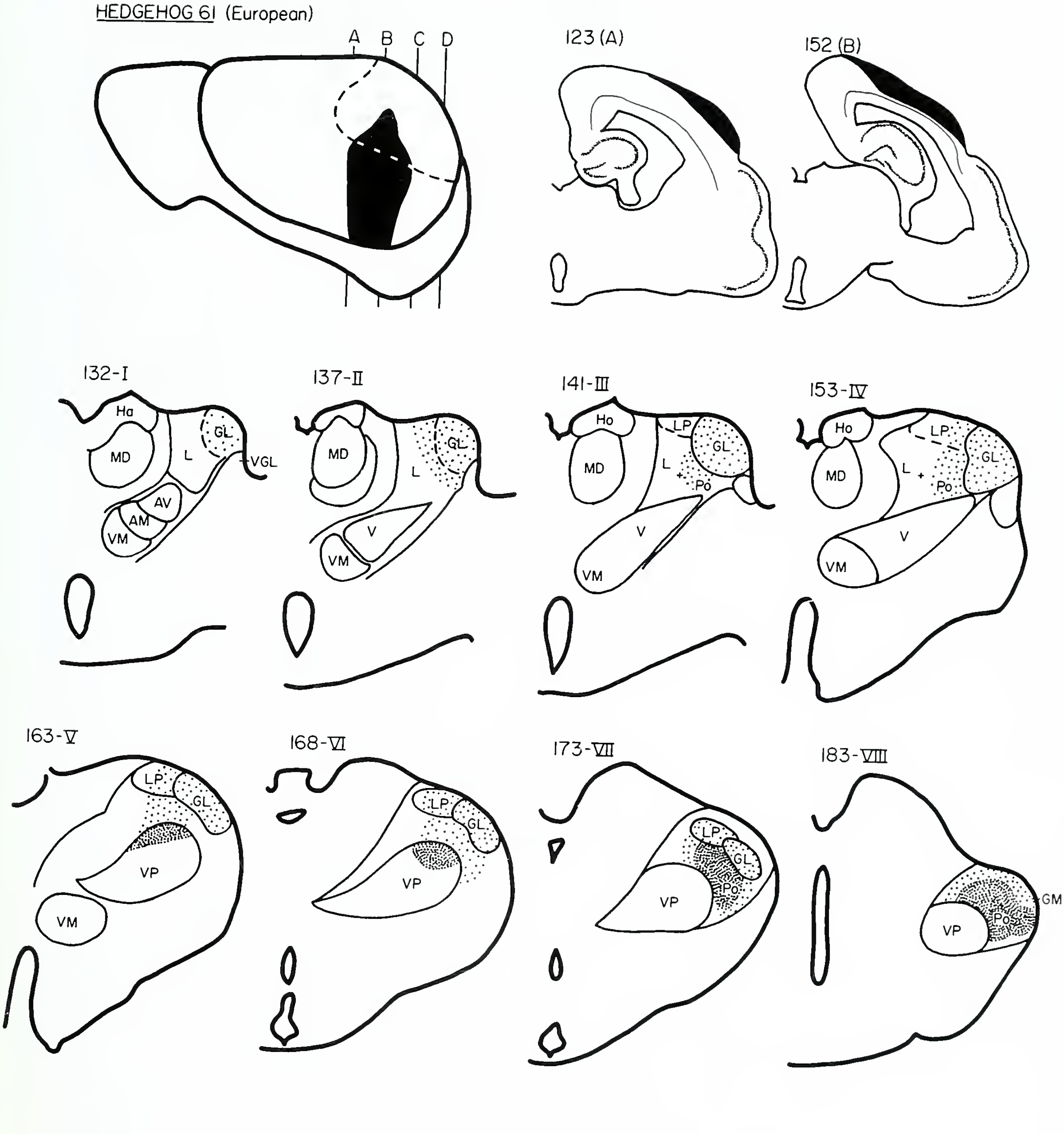

HEDGEHOG 61 (European)
A B C D
123 (A)
152 (B)
132-I
Ha
MD
L
GL
VGL
AV
AM
VM
137-II
MD
GL
L
V
VM
141-III
Ho
LP
GL
MD
L
Po
V
VM
153-IV
Ho
LP
GL
MD
L
Po
V
VM
163-V
LP
GL
VP
VM
168-VI
LP
GL
VP
173-VII
LP
GL
Po
VP
183-VIII
GM
Po
VP

Figure 18. Cortical Lesion and Thalamic Degeneration in Hedgehog 105. The lesion removes approximately the anterior three-fourths of the visual area. Although the entire lateral geniculate is affected, the degeneration is not severe. The slight degeneration in anterior GL reflects the sparing of posterior visual cortex. In thalamic Levels IV and V the degeneration is most severe in ventral GL, corresponding to the fact that the posterior extent of the lesion is greatest along the medial boundary of the visual area.

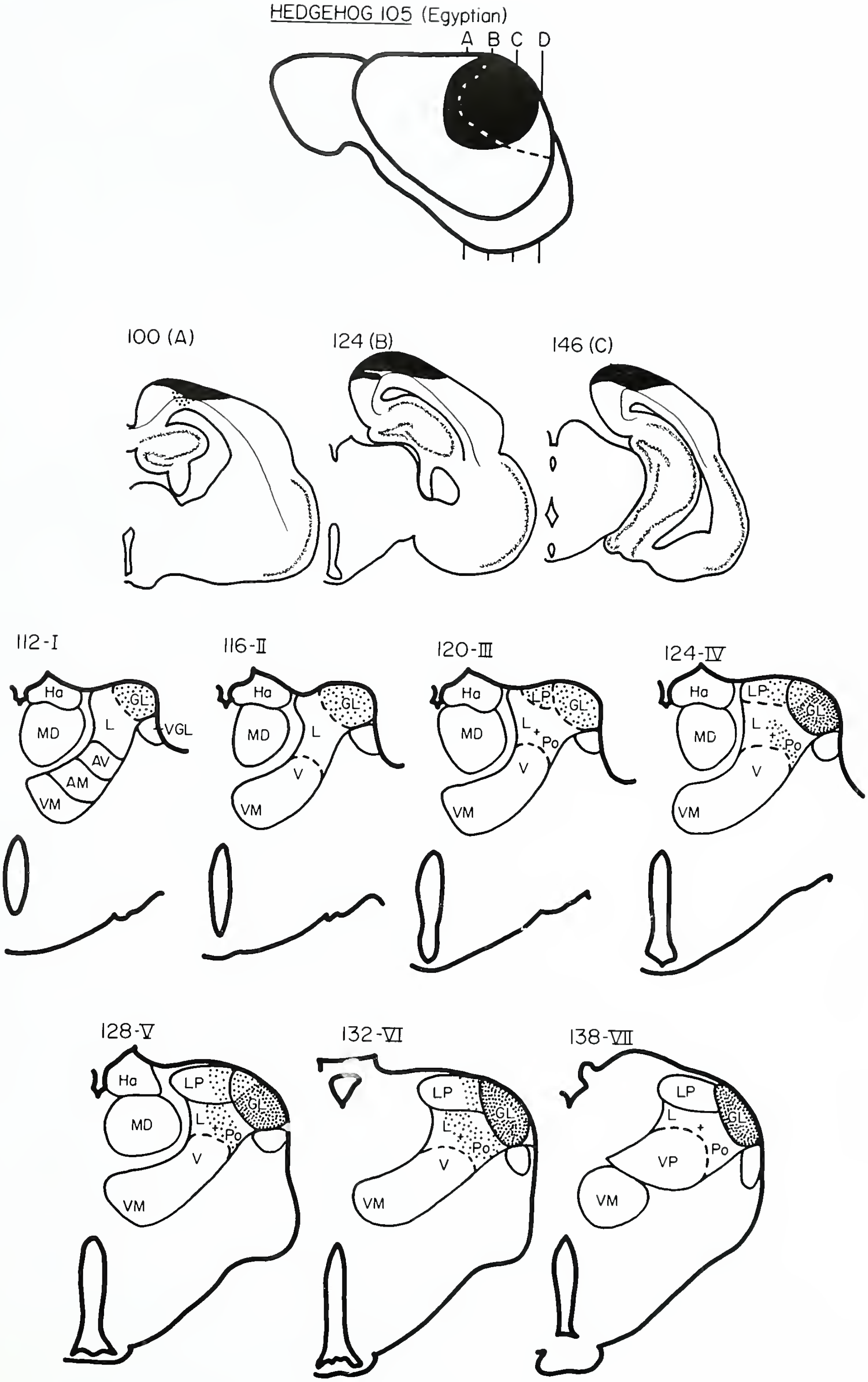

HEDGEHOG 105 (Egyptian)
A B C D
100 (A)
124 (B)
146 (C)
112-I
Ha
MD
L
GL
VGL
AV
AM
VM
116-II
Ha
MD
L
GL
V
VM
120-III
Ha
LP
GL
MD
L
Po
V
VM
124-IV
Ha
LP
GL
MD
L
Po
V
VM
128-V
Ha
LP
GL
MD
L
Po
V
VM
132-VI
LP
GL
L
Po
V
VM
138-VII
LP
GL
L
Po
VP
VM

Figure 19. Cortical Lesion and Thalamic Degeneration in Hedgehog 108. The lesion removes the anterior visual area. The degeneration is only slight in the dorsal part of anterior GL reflecting the fact that the lesion spares a posterolateral segment of the visual area. In spite of the size of the lesion, no part of GL is severely degenerated.

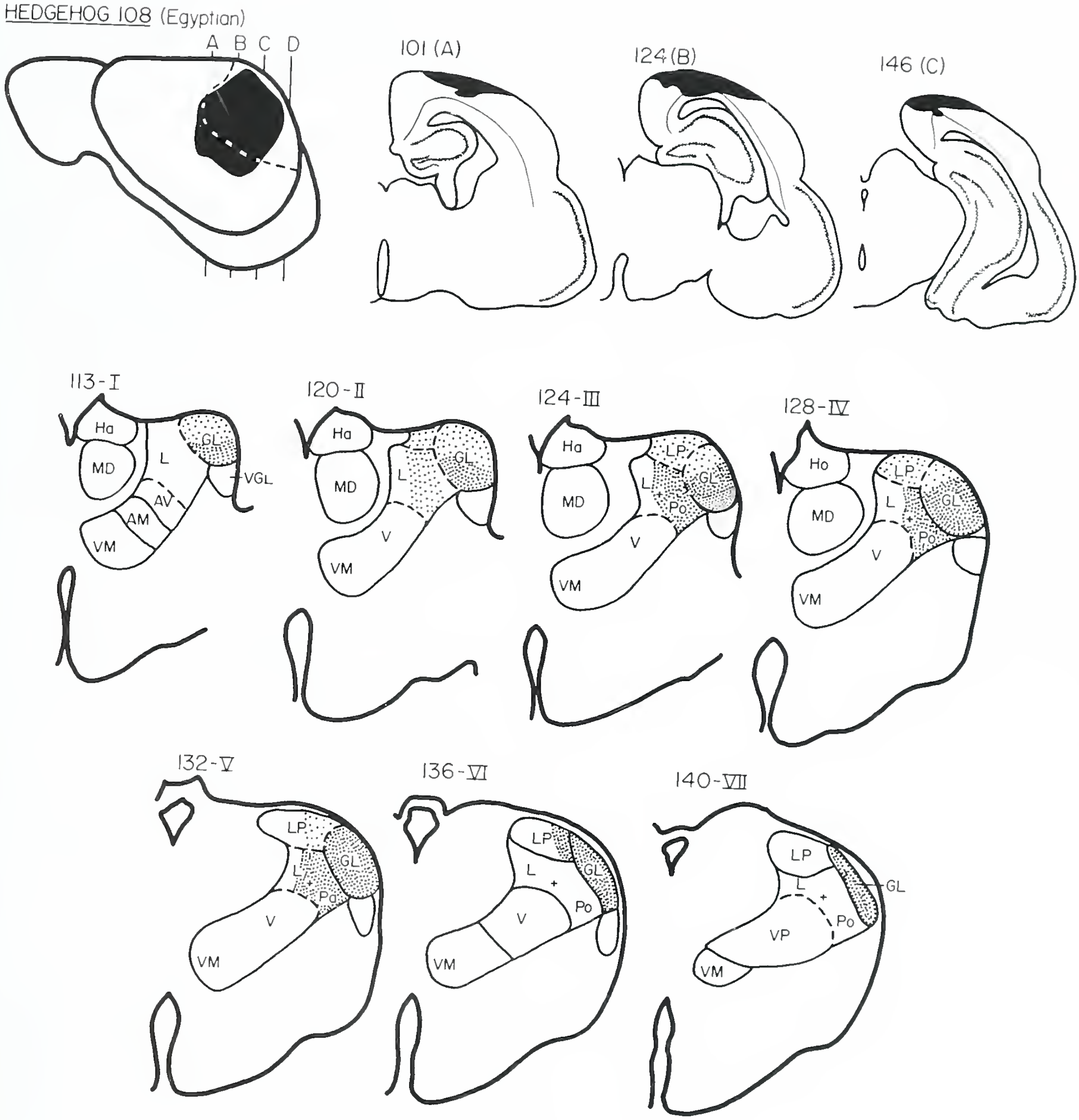

HEDGEHOG 108 (Egyptian)
A B C D
101 (A)
124 (B)
146 (C)
113-I
Ha
MD
L
GL
VGL
AV
AM
VM
120-II
Ha
MD
L
GL
V
VM
124-III
Ha
LP
GL
L
Po
MD
V
VM
128-IV
Ho
LP
L
GL
MD
Po
V
VM
132-V
LP
GL
L
Po
V
VM
136-VI
LP
GL
L
Po
V
VM
140-VII
LP
L
GL
Po
VP
VM

Figure 20. Cortical Lesion and Thalamic Degeneration in Hedgehog 112. The slight degeneration in the dorsal part of anterior GL corresponds to the spared portions of posterolateral visual cortex.

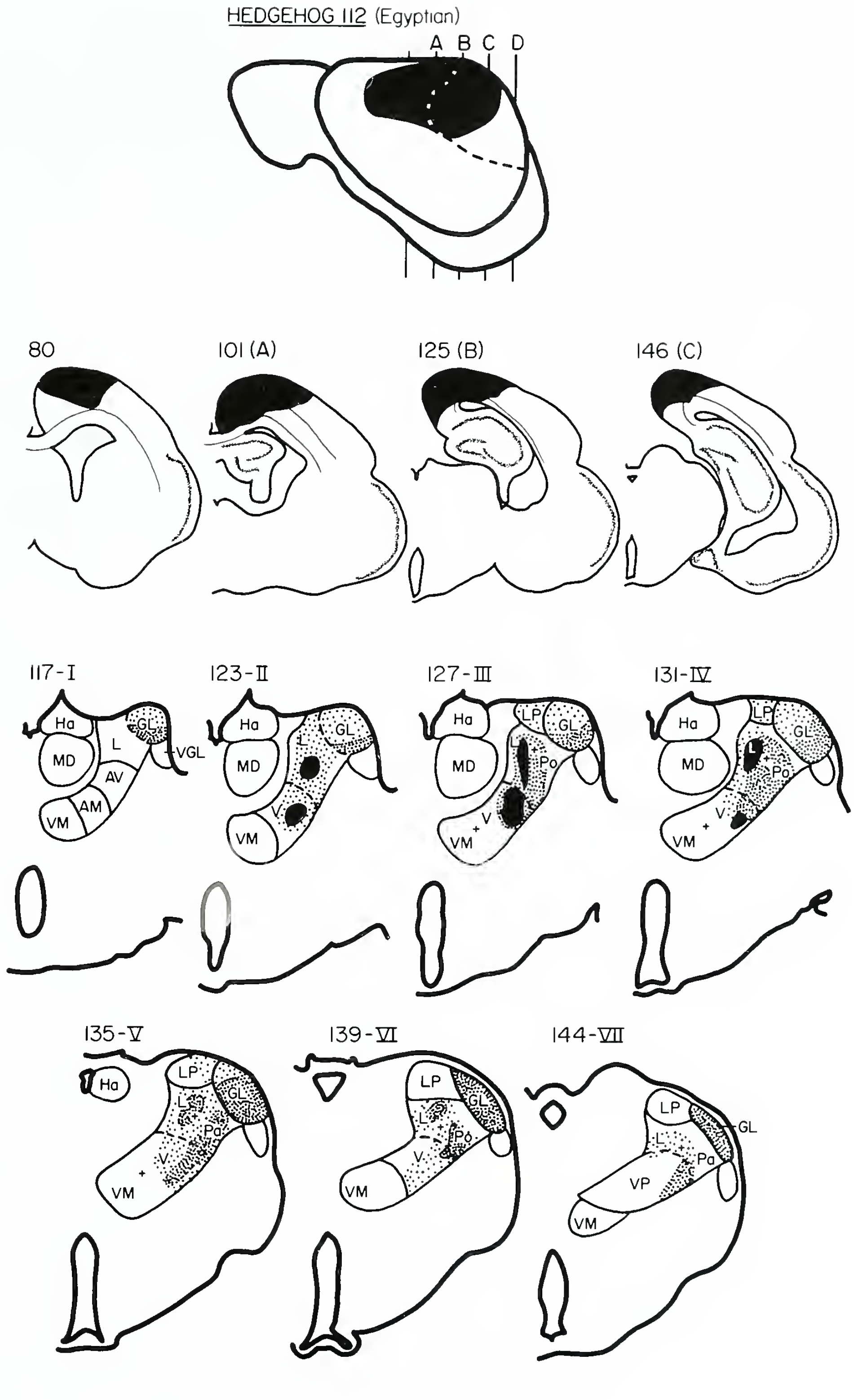
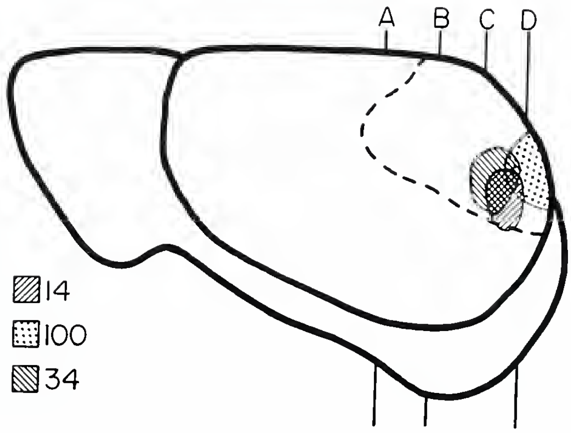

HEDGEHOG 112 (Egyptian)
A B C D
80
101 (A)
125 (B)
146 (C)
117-I
Ha
GL
L
VGL
MD
AV
AM
VM
123-II
Ha
GL
MD
V
VM
127-III
Ha
LP
GL
MD
L
Po
V
VM
131-IV
Ha
LP
GL
MD
L
Po
V
VM
135-V
Ha
LP
GL
L
Pa
V
VM
139-VI
LP
GL
L
Po
V
VM
144-VII
LP
GL
L
Pa
VP
VM

Figure 21. A Composite of Lesions Which Produced Only Slight Degeneration in the Lateral Geniculate.


A
B
C
D
14
100
34

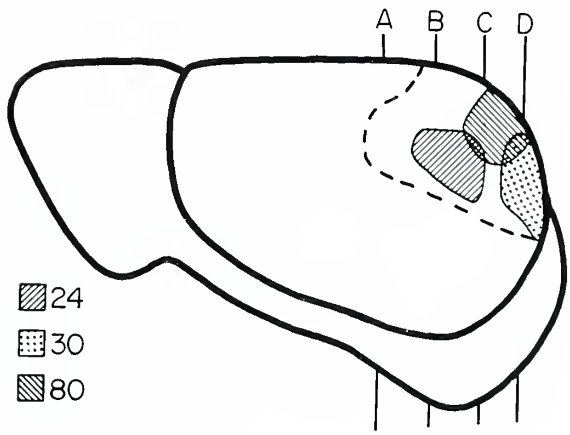

A
B
C
D
24
30
80

Figure 22. Cortical Lesion and Thalamic Degeneration in Hedgehog 24. This is a small lesion confined to visual cortex which produced only slight degeneration in GL.

HEDGEHOG 24 (European)

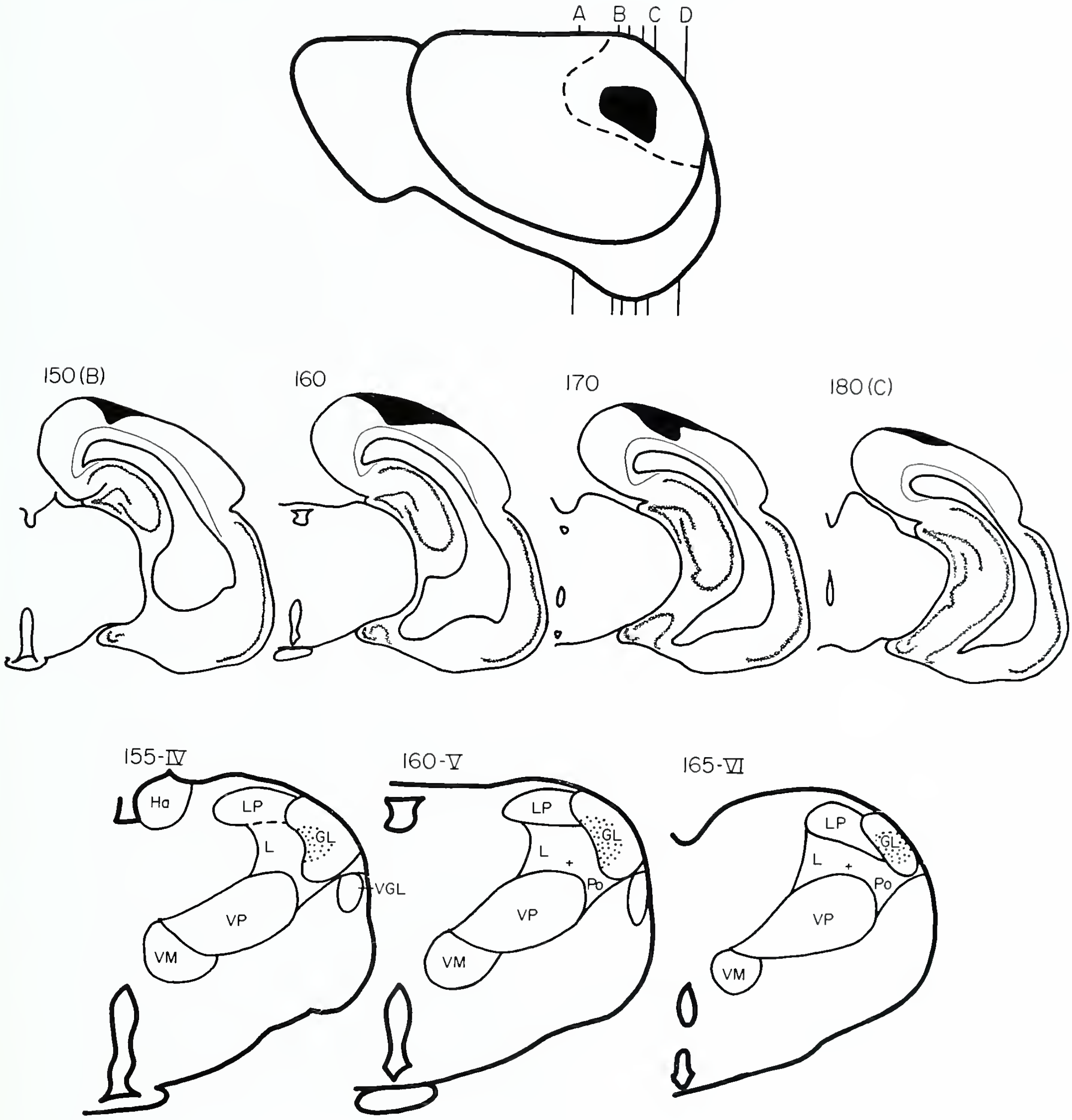
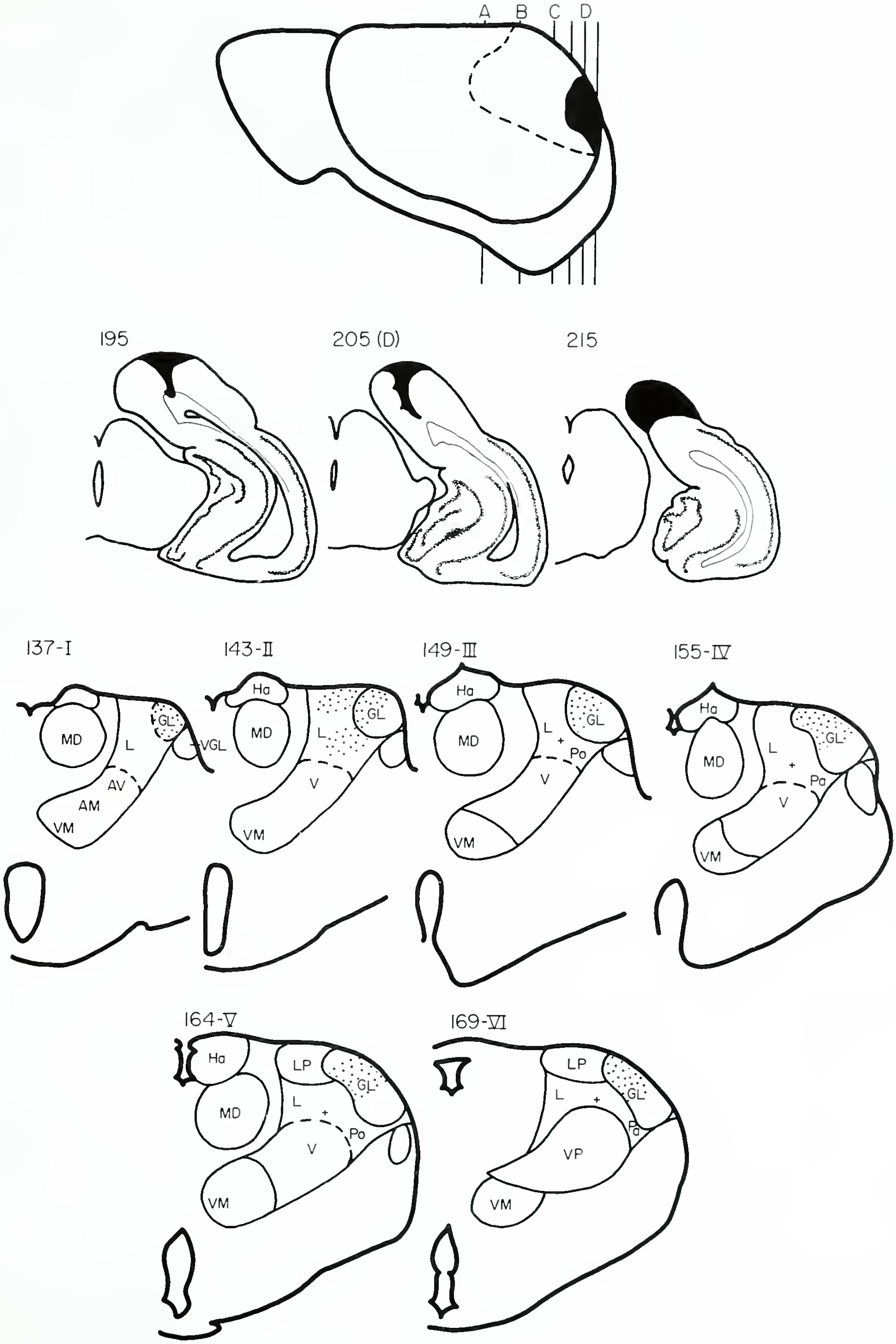


Figure 23. Cortical Lesion and Thalamic Degeneration in Hedgehog 30. This is a small lesion confined to visual cortex. Although slight, the degeneration extends throughout a large part of GL.

HEDGEHOG 30 (European)



BEHAVIORAL METHODS

The behavioral experiments now to be described were based on ten hedgehogs all of which were trained to visual discrimination problems before and after cortical ablations.

Procedures for Maintaining the Animal Colony

Since hedgehogs possess several features which distinguish them from the mammals most commonly used in behavioral experiments, several special procedures which were important for maintaining the colony are of interest.

Being primarily crepuscular and nocturnal animals, the hedgehogs were usually inactive during the day. Often the body temperature of the animals decreases during these inactive hours making it a prolonged and difficult process to arouse them to a state suitable for behavioral experiments. Consequently, for convenience the animals were maintained on a reversed day-night cycle. The windows of the colony room were covered and an automatic timer turned the room lights out

at 7 a.m. and on again at 7 p.m.

The hedgehogs were voracious eaters and tended to gain excessive weight in the laboratory. To counteract this tendency the animals were maintained on a rigorous diet consisting of an ounce of horsemeat mixed with a vitamin supplement, one or two tablespoons of ground fruit and several pieces of Purina cat chow. In addition, a revolving exercise wheel larger than but similar in design to the type available commercially for hamsters was used extensively by the animals and was found to be useful for preventing obesity. The diet and exercise wheels proved sufficient to maintain the animals in a healthy and active state for a period of several years.

Food deprivation in preparation for training presented a particular problem with hedgehogs. The animals proved quite sensitive to the absence of food; after as short a period as one day of deprivation, they would often become inactive and even approach a hibernating condition, characterized by a low body temperature and sluggishness. After experimenting with the animals under a variety of conditions, we found that they would continue to work for long periods in a behavioral experiment without food deprivation for a highly preferred reward. For the Egyptian hedgehogs the reward consisted of a moth larva and for the European species, a small piece of horsemeat.

The wild hedgehogs obtained from an animal dealer were extremely sensitive to stimuli such as the handling, noise and odors which are normally associated with a behavioral apparatus and consequently required considerable taming before training could be initiated. Taming of the wild animals was accomplished for the most part by simultaneous feeding and handling. Three of the ten animals trained in the present experiments were wild (Cases 21, 29, 110); the remaining seven were born and raised in the colony.

The Egyptian hedgehogs but not the European species were bred in the laboratory. The Egyptian hedgehogs appeared to breed throughout the year, usually producing litters numbering three to four animals. Mating was accomplished simply by putting the two animals together in a cage for a period of about one hour on each of several days. The exact time of mating could be easily determined since it was always preceded by a distinct courtship behavior consisting primarily of rapid circling of the female by the male. After mating, the male and female were always caged separately.

The gestation period varied from thirty to thirty-six days. A wooden box enclosed except for a small hole for an entrance was provided for a nest. During the first week following birth, if the nest is disturbed the mother becomes

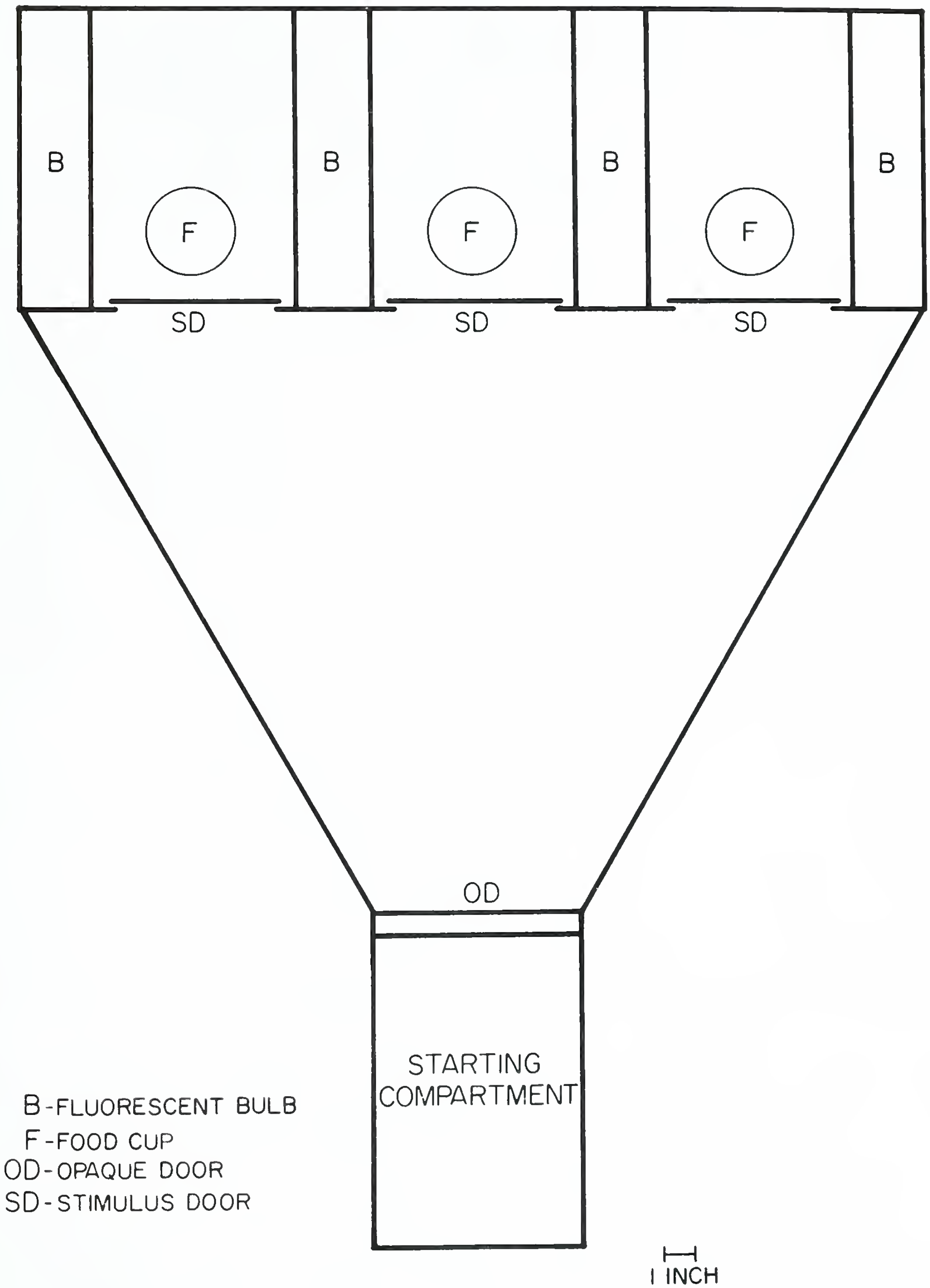
extremely excited and may devour the young. After the first week, however, the young can be removed from the nest, handled and then returned and the mother will continue to nurse them. By three months, the animals are mature and, if handled daily until this time, they are very tame.

Apparatus

Two apparatuses were used in the present experiments. The first was the three choice Yerkes type box diagramed in Figure 24. The apparatus was made of plexiglass and painted black. The animals were released from the starting compartment by raising the opaque sliding door which, between trials, blocked the exit. The animals could then obtain a reward at the opposite end of the apparatus by approaching and pushing open the correct one of the three counterbalanced stimulus doors which were situated directly in front of the food cups. The doors were hinged at their upper edge to the frame of the apparatus and, when pushed by the animal, would swing backward revealing the food cups.

Each counterbalanced door was opaque except for a 4 in. by 4 in. glass covered opening directly behind which the stimuli were displayed. The stimuli consisted of 5 in. by 5 in. cards made of opaque black and translucent white paper

Figure 24. Diagram of Three Choice Discrimination Apparatus.


B
B
B
B
F
F
F
SD
SD
SD
OD
STARTING COMPARTMENT
B-FLUORESCENT BULB
F-FOOD CUP
OD-OPAQUE DOOR
SD-STIMULUS DOOR
1 INCH

embedded between two plates of 1 mm. thick Kodak glass. Mounting the cards in glass insured that the stimuli were always flat and also permitted periodic cleaning. The cards were inserted into the apparatus behind the glass covered door openings by sliding them into a frame mounted on the back of each door. The glass plate which covered the opening prevented the animals from coming into direct contact with the stimuli. Throughout the experiments the apparatus was located in a darkened room and the stimuli were illuminated by light transmitted through the white sectors of the cards from the four fluorescent bulbs situated behind the doors.

At the outset of the present experiments seven animals were trained and tested in the three choice apparatus. For each discrimination, two of the stimuli were identical; the animals were trained to respond to the third, dissimilar stimulus. Shortly after postoperative training began, however, it became apparent that for animals with cortical lesions a three choice pattern discrimination would be considerably more difficult than the same discrimination involving only two choices (see, for example, Case 21, Fig. 30, Page 95). Consequently, after surgery the training situation for all animals was eventually changed to a two choice discrimination. The number of doors in the apparatus just described was reduced simply by permanently darkening the left stimulus

door with a black card. Subsequently, three animals which began training later in the course of the experiments were able to receive their training in a two choice apparatus (Cases 48, 110, 109, Figs. 32, 33, 34, Pages 99, 101, 103). This apparatus was similar to the three choice Yerkes box except that it consisted of two rather than three stimulus doors and the light which illuminated the stimuli was provided by a pair of projectors, one behind each door.

As the experiment turned out, the animals which failed to relearn were all trained in this second apparatus; therefore, the similarities between the two behavioral situations should be emphasized. In terms of the learning curves obtained and equivalence test results, no differences were found between the two apparatuses. In addition, animals trained to a pattern discrimination in one apparatus were found to transfer without further training to the same discrimination in the second box. The most important factor is the fact that each hedgehog served as its own control, since all animals were trained both before and after surgery. The estimate of the behavioral deficit therefore is derived from comparing the pre- and postoperative performances of each individual animal.

Training Procedures

Initially each animal was trained to approach and push open the stimulus doors upon release from the starting compartment. The response was rewarded with the food situated immediately behind each door. After the animals became proficient at opening the doors, training on a series of visual discrimination problems was begun.

Throughout the discrimination training, all doors were baited with food and the incorrect door containing the negative stimulus was locked. The animals were trained to approach and push open the door displaying the positive stimulus and to avoid the negative stimulus. For the three choice situation, the position of the positive stimulus on successive trials was determined by a series of numbers which were random except that the same door could not be positive more than three consecutive times. In the two choice situation, the sequence was determined by the Gellerman series of random positions (Gellerman, 1933).

A trial began when the animal was released from the start box. If the animal pushed open the correct door, it was allowed to eat the reward before being returned to the starting compartment for the next trial. If, on the other

hand, the incorrect door was pushed, the lock prevented the door from opening. The animal was picked up before it could turn to approach a second door and returned to the start box. The trial was scored as incorrect. Following the incorrect response, however, the positions of the stimuli were not changed and the trial was continued by releasing the animal from the starting compartment a second or even a third time until the correct door was approached and opened. Only then was a new trial initiated.

The animals were given an average of ten trials during each session. Criterion was reached when the animal made a score of nineteen correct responses for two consecutive ten trial sessions.

Discrimination problems. The animals received training on three discrimination problems. The first problem was light versus no-light. The stimuli consisted of translucent white and opaque black cards. All animals were trained to choose the white card. The light versus no-light discrimination served to adapt the animals more thoroughly to the training situation, as well as postoperatively, to demonstrate that they could still form a conditioned response to a visual stimulus.

Following the light versus no-light discrimination, each animal was trained to discriminate between horizontal

and vertical stripes. The stimulus cards were made of alternating 0.25 in. stripes of black and white paper. Five animals were trained to choose the horizontal stripes and the remaining five the vertical.

The third problem was upright versus inverted triangles. The stimuli were white equilateral triangles centered on a black background. The sides of the triangles measured 2.5 in.

Preoperatively, each hedgehog was required to reach the learning criterion on the horizontal versus vertical stripes discrimination before training was begun on the triangle problem. Postoperatively, many of the animals attained a level of performance well above chance on the stripe discrimination but were unable to reach criterion. These animals were given the triangle discrimination after no further improvement in performance on the stripe problem could be expected. The postoperative animals which failed to relearn the stripe discrimination did not receive subsequent training on the triangle problem since the results indicated that the latter task is the more difficult for hedgehogs, both before and after surgery.

<u>Equivalence tests</u>. Since animals may solve a particular discrimination problem on the basis of a variety of cues, the attainment of a criterion score by itself was not considered to be a sufficient description of the hedgehog's vision either before or after surgery (Klüver, 1933, 1942; Lashley, 1939).

Consequently, in addition to the discrimination training a series of equivalence tests were given to each animal (Fig. 55, Page 139). After criterion was attained on a pattern discrimination problem, a series of test sessions was given. Each test session began with two preliminary trials on the original training task. If an incorrect response was made on one of these trials, the remainder of the sessions was devoted to further training. If, on the other hand, the animal responded correctly on each of the initial training trials, an equivalence test was given on the third trial. For the remainder of the session, the equivalence test was alternated with training trials. Up to twenty-five trials were given in a test session depending on the motivation of the animal. If, however, the animal made more than one error within five presentations of the original training problem, the session was discontinued and the results obtained from the equivalence tests presented that day were disregarded.

Special Postoperative Training Procedures

Since the primary purpose of the behavioral experiments was to determine the ability of the hedgehog to discriminate patterns after cortical lesions, two additional training

tasks were developed in the course of the postoperative training in a special effort, either to improve or to study in more detail the performance of retarded animals.

The rationale for the first task came from preliminary results of an electrophysiological investigation of the projection of the visual field on the cortex of the hedgehog (Kaas, Hall and Diamond, experiments in progress). These results indicated that a large proportion of the hedgehog visual cortex is devoted to input from the lower visual field. In an attempt to improve the scores of animals which were unable to reach or maintain a criterion level of performance on the triangle problem, several sessions of training were introduced using stimuli with the triangles lowered 0.5 in. on the card. In the illustrations the sessions on which this second triangle task was presented is indicated by the break in the abscissa.

Secondly, following postoperative triangle training, several of the animals were retrained to the stripe discrimination problem. The purpose of the additional stripe training was to permit the subsequent presentation of a more extensive series of equivalence tests.

Surgical and Histological Procedures

The surgical and histological procedures were identical to those used in the anatomical experiments except that all behavioral hedgehogs received one stage bilateral cortical ablations. Following surgery, a recovery period of at least two weeks preceded the beginning of postoperative training.

BEHAVIORAL RESULTS

The main behavioral result is derived from the postoperative performances on the pattern discrimination problems: the ten hedgehogs formed two distinct groups. Seven of the animals were able to relearn at least one pattern discrimination whereas the remaining three failed to relearn. Subsequent examination of the brains revealed that the behavioral difference between the two groups could be explained by differences in the cortical lesions. The purpose of this section is first, to show the difference between the postoperative performances of the two groups and second, to relate this difference to the cortical lesions. What emerges from this analysis is a definition of the cortical structure in the hedgehog which is necessary for pattern discrimination.

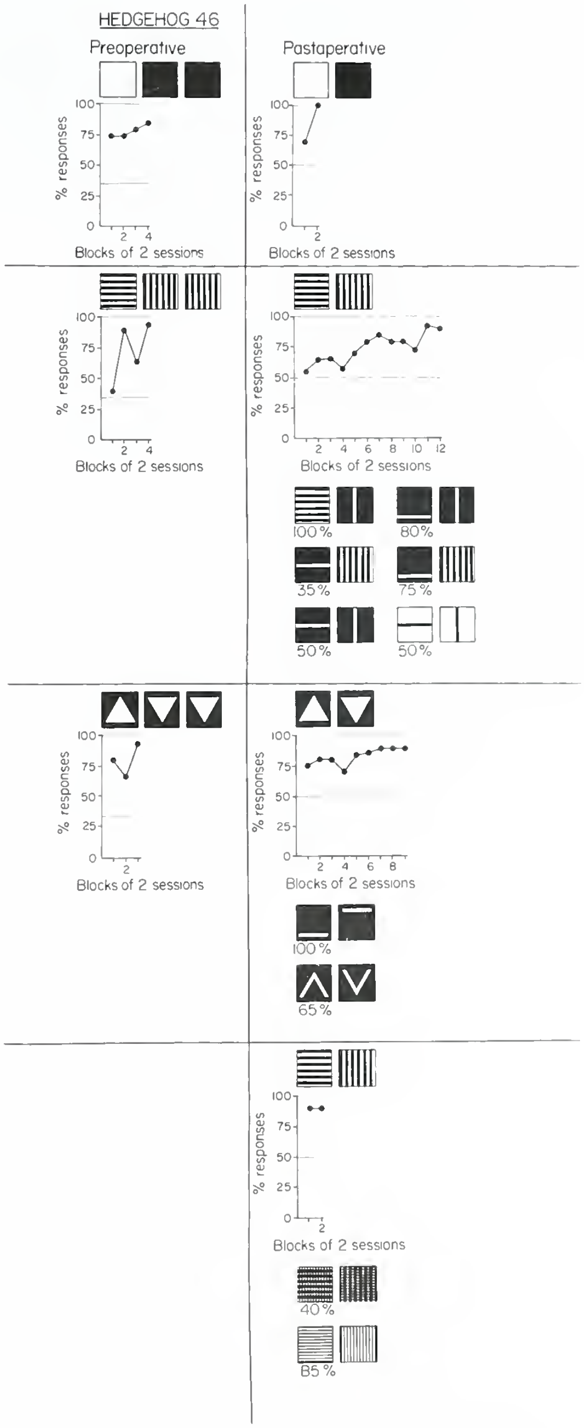
Postoperative Relearning

Figures 25 to 34 present the learning curves and

equivalence test results for each of the ten animals. The learning curves indicate that postoperatively, seven hedgehogs were able to relearn at least the horizontal versus vertical stripes discrimination (Cases 46, 44, 29, 43, 47, 21 and 41, Figs. 25 to 31). Five of the seven animals eventually reached criterion on this task (Cases 46, 44, 29, 43 and 21, Figs. 25, 26, 27, 28, 30). The remaining two animals, Hedgehogs 47 and 41, although unable to reach criterion, maintained a level of performance well above that expected from chance throughout most of their postoperative training (Figs. 29, 31). Following the stripe discrimination, five of the seven animals were trained to the upright versus inverted triangle task (Cases 46, 44, 29, 43, 47, Figs. 25 to 29). Three of the five, Hedgehogs 46, 44 and 29, were able to attain a level of performance much higher than chance and two, Cases 46 and 29, eventually reached criterion on this second problem.

In the second group, none of the animals relearned (Cases 48, 110 and 109, Figs. 32 to 34). Two hedgehogs, 48 and 110, showed no signs of improving above a chance level of performance after fifty sessions of retraining on the horizontal versus vertical stripes discrimination (Figs. 32, 33). Hedgehog 109 received even more extensive postoperative retraining but the performance was still at a chance level

Figure 25. Behavioral Results for Hedgehog 46. Postoperatively, the animal was able to attain criterion on both the stripe and triangle discriminations. Following postoperative training to triangles, the animal was retrained a second time to the stripe discrimination in order that the final pair of equivalence tests could be presented.



HEDGEHOG 46
Preoperative
Postoperative
% responses
Blocks of 2 sessions
100%
80%
35%
75%
50%
50%
100%
65%
40%
85%

Figure 26. Behavioral Results for Hedgehog 44. Postoperatively, Hedgehog 44 reached criterion on the horizontal versus vertical stripes discrimination. The break in the learning curve for this task indicates a change from a three to a two choice discrimination. An above chance level of performance was maintained on the triangle problem but after over 50 sessions of retraining the animal failed to reach criterion. The break in the abscissa for the postoperative triangle training indicates sessions in which the animal received special training with the triangles lowered on the card. Following postoperative training to triangles, the animal was returned to the stripe discrimination problem in order that a final series of equivalence tests could be presented.

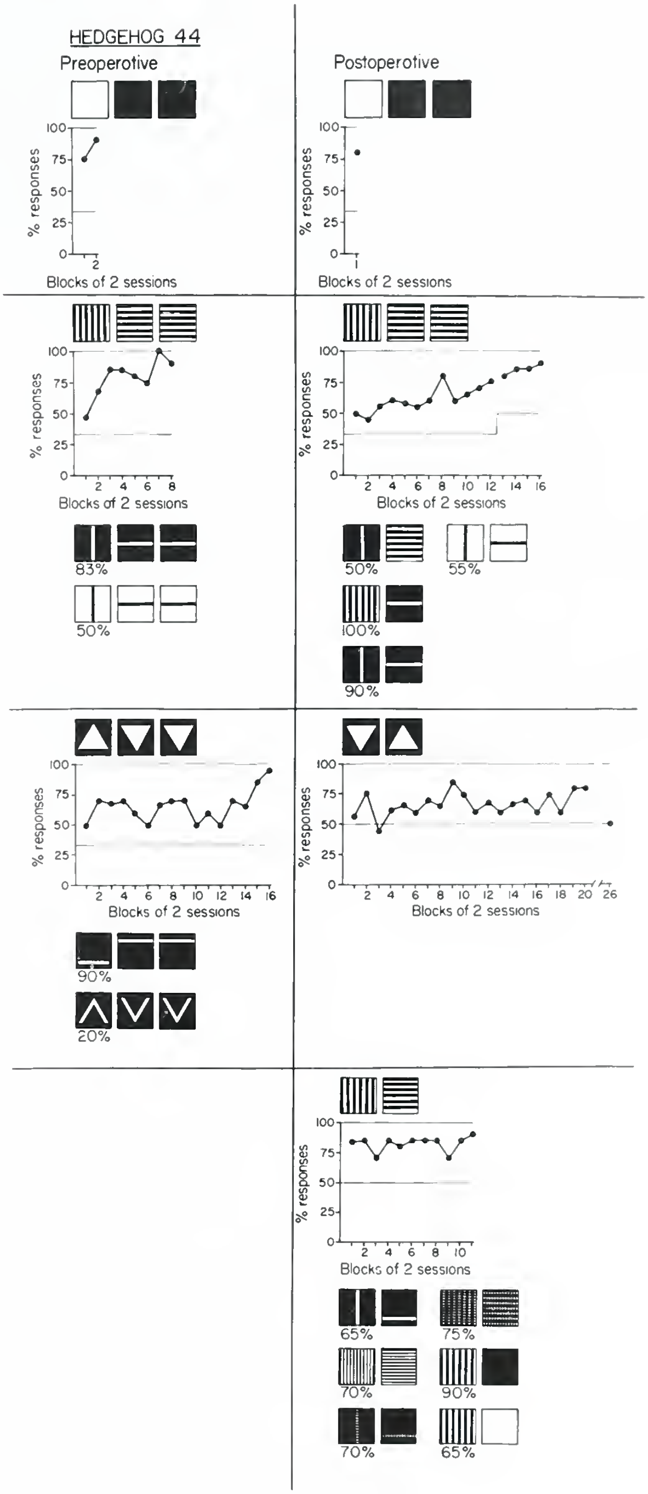

HEDGEHOG 44
Preoperative
Postoperative
% responses
100
75
50
25
0
Blocks of 2 sessions
83%
50%
50%
55%
100%
90%
90%
20%
65%
75%
70%
90%
70%
65%

Figure 27. Behavioral Results for Hedgehog 29. Postoperatively, Hedgehog 29 eventually reached criterion on both the stripe and triangle discrimination problems. The breaks in the performance curve for postoperative stripe training indicate changes from a three to a two choice discrimination. Following postoperative training to triangles, this animal was retrained a second time to the stripe discrimination in order that the final series of equivalence tests could be presented.

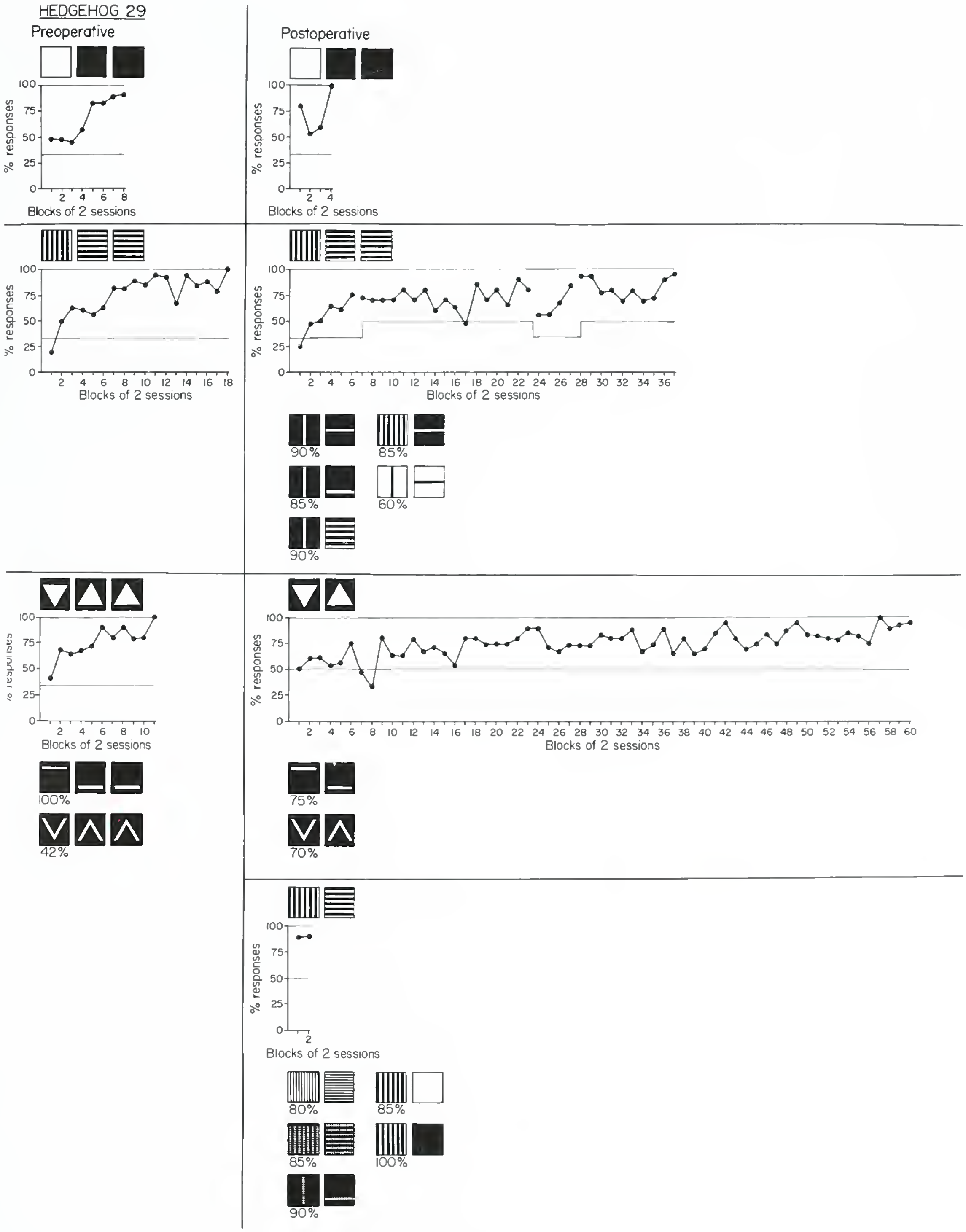

HEDGEHOG 29
Preoperative
Postoperative
% responses
Blocks of 2 sessions
90%
85%
85%
60%
90%
100%
42%
75%
70%
80%
85%
85%
100%
90%

Figure 28. Behavioral Results for Hedgehog 43. Hedgehog 43 was able to reach criterion postoperatively on the horizontal versus vertical stripes discrimination but failed on the triangle problem. The break in the abscissa for the learning curve which represents the postoperative performance on the triangle task indicates sessions in which the animal received special training with the triangles lowered on the card. Following the postoperative triangle training, Hedgehog 43 was returned to the stripe discrimination problem in order that the final series of equivalence tests could be presented.

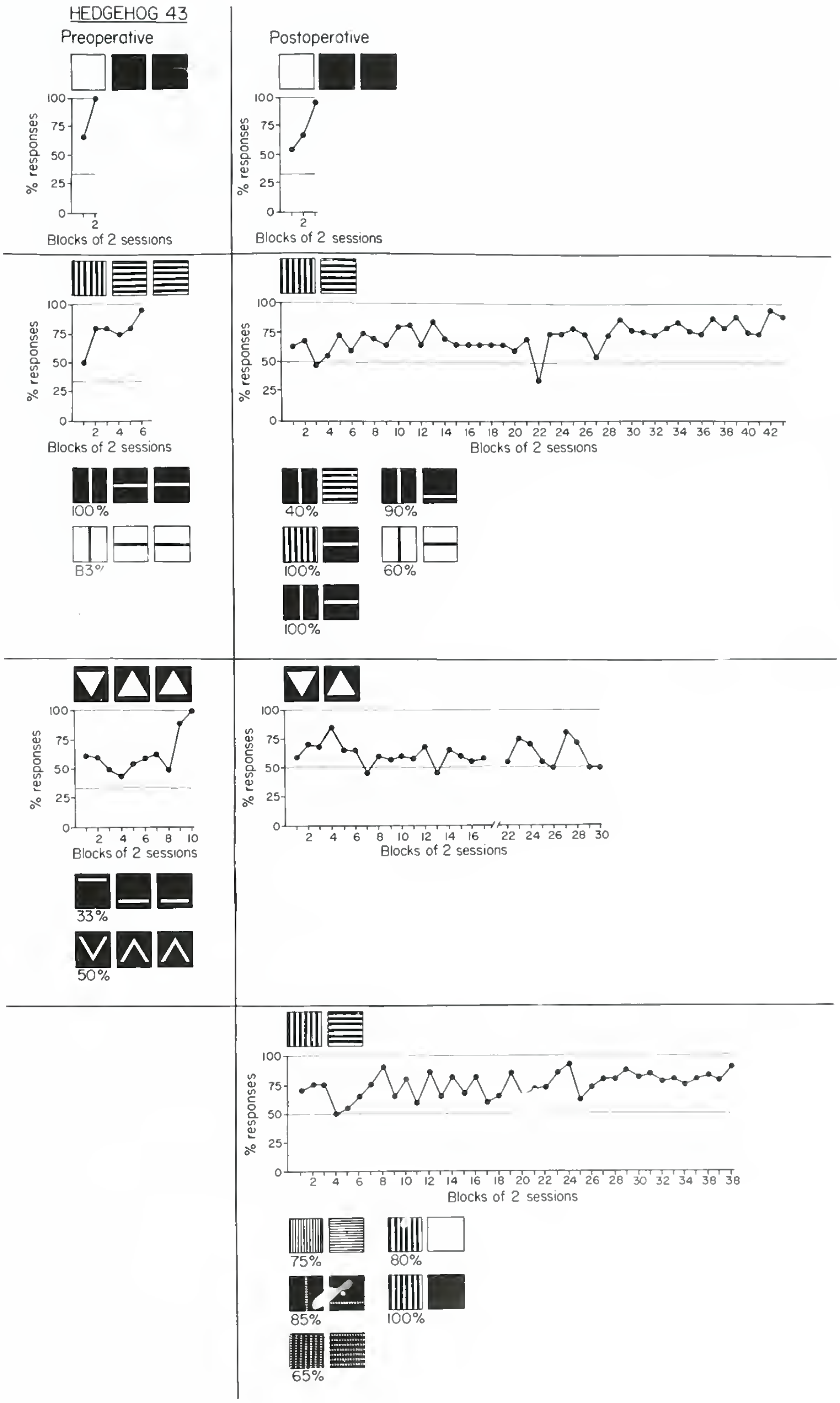

HEDGEHOG 43
Preoperative
Postoperative
% responses
Blocks of 2 sessions
100%
83%
40%
90%
100%
60%
100%
33%
50%
75%
80%
85%
100%
65%

Figure 29. Behavioral Results for Hedgehog 47. Postoperatively, Hedgehog 47 was able to maintain a level of performance well above chance on the horizontal versus vertical stripes discrimination but did not reach criterion after almost 100 sessions of retraining. The animal could not maintain an above chance level of performance on the triangle discrimination. The break in the abscissa for the triangle problem indicates sessions in which special training was given with the triangles lowered on the card.

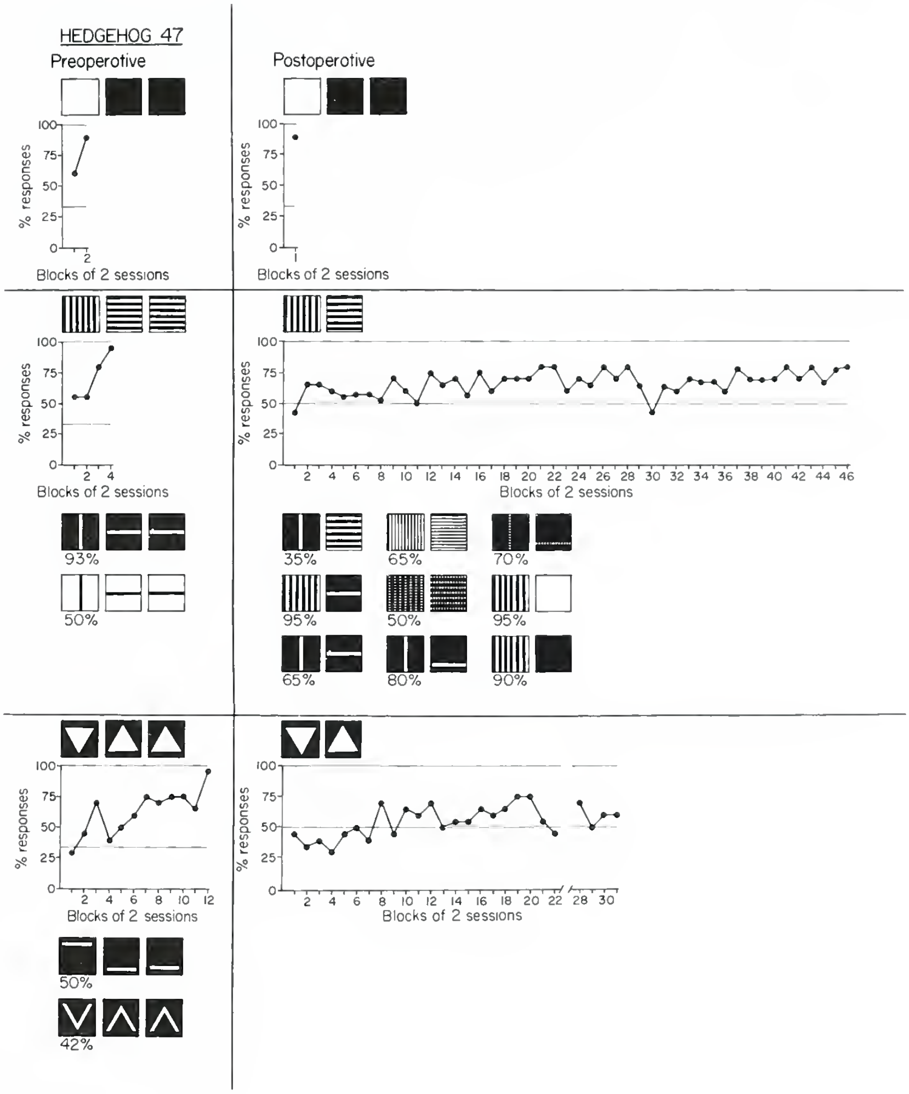
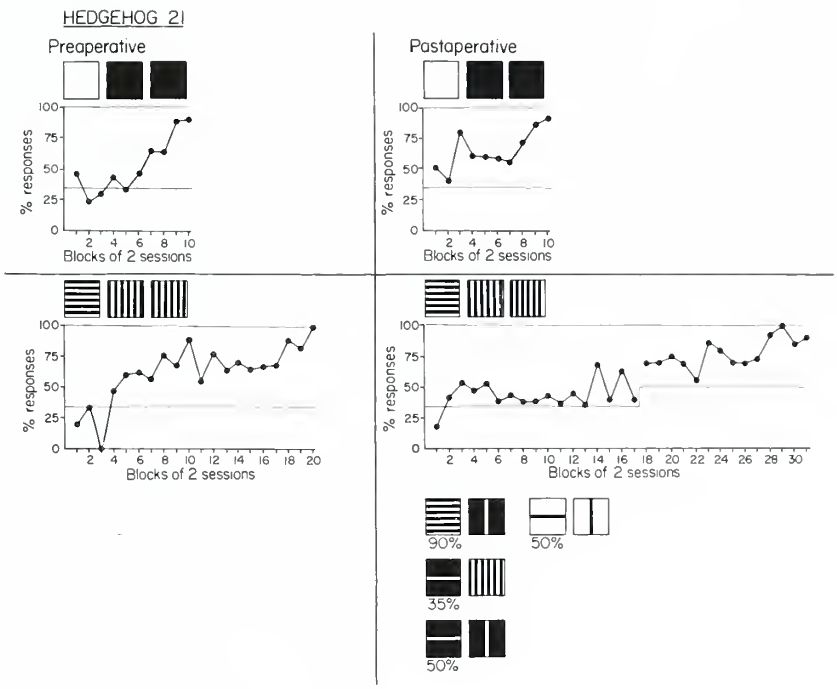
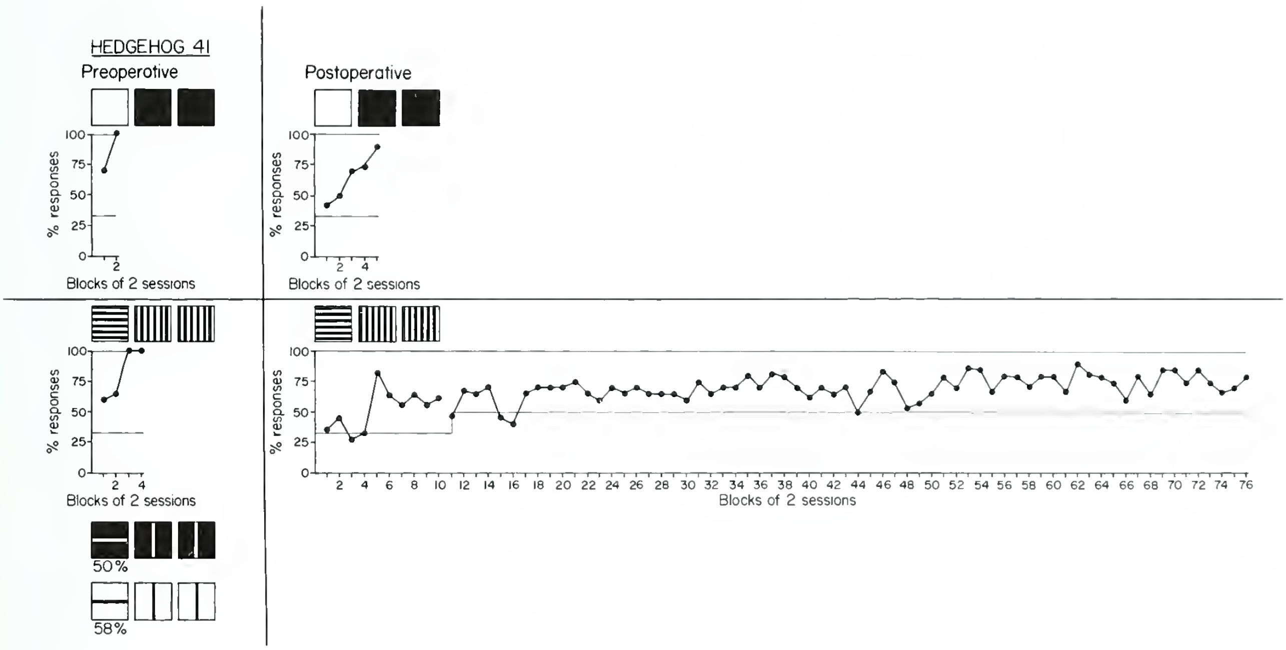

HEDGEHOG 47
Preoperotive
Postoperotive
% responses
Blocks of 2 sessions
93%
50%
35%
65%
70%
95%
50%
95%
65%
80%
90%
50%
42%

Figure 30. Behavioral Results for Hedgehog 21. Postoperatively, Hedgehog 21 reached criterion on the horizontal versus vertical stripes discrimination. The break in the postoperative learning curve for the stripes discrimination indicates a shift from the three to a two choice situation. Hedgehog 21 died before postoperative training to triangles could be initiated. The preoperative learning curve for triangles is therefore not presented.



HEDGEHOG 21
Preoperative
Postoperative
% responses
Blocks of 2 sessions
90%
50%
35%
50%

Figure 31. Behavioral Results for Hedgehog 41. Postoperatively, this animal was able to maintain an above chance level of performance on the horizontal versus vertical stripes discrimination problem but failed to reach criterion after 152 sessions of retraining. The break in the performance curve for this task indicates the change from a three choice to a two choice discrimination. The animal died before equivalence tests or triangle training could be administered. The preoperative triangle training is therefore not shown.



HEDGEHOG 41
Preoperotive
Postoperative
% responses
100
75
50
25
0
Blocks of 2 sessions
50%
58%

Figure 32. Behavioral Results for Hedgehog 48. After 50 postoperative sessions this animal was still performing at a chance level on the vertical versus horizontal stripes discrimination. Since the animal failed to relearn the stripe discrimination, there was no postoperative training to the triangle problem.

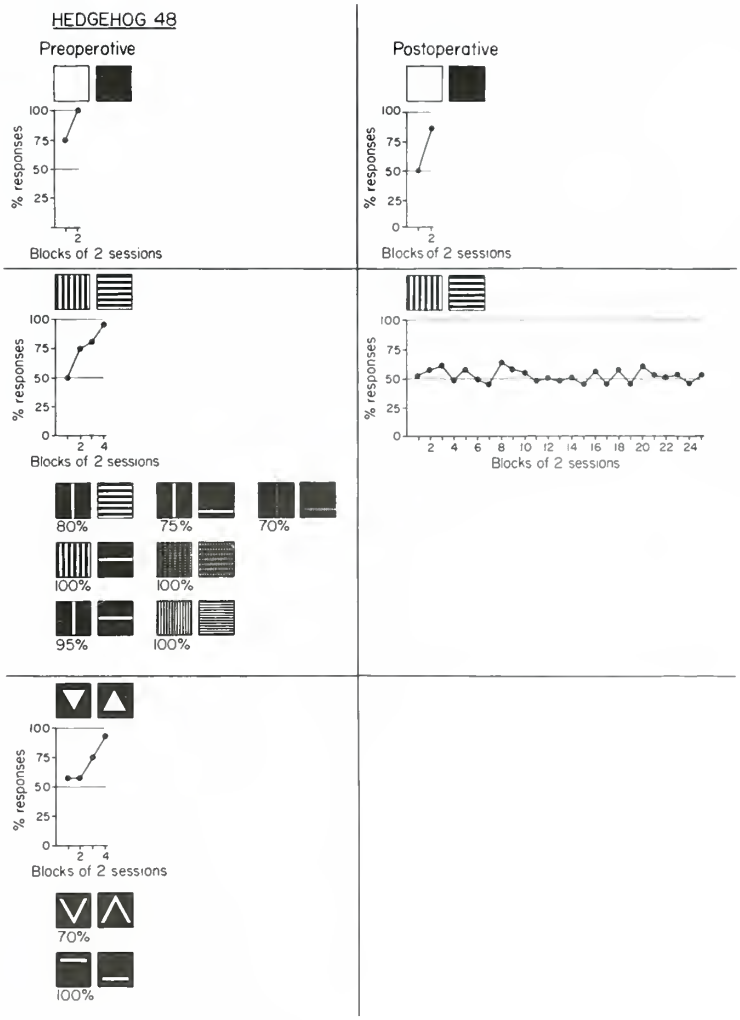

HEDGEHOG 48
Preoperotive
Postoperative
% responses
Blocks of 2 sessions
80%
75%
70%
100%
100%
95%
100%
70%
100%

Figure 33. Behavioral Results for Hedgehog 110. After 50 postoperative sessions this animal was still performing at a chance level on the horizontal versus vertical stripes discrimination problem. Since the animal failed to relearn the stripe discrimination there was no postoperative training on the triangle problem.

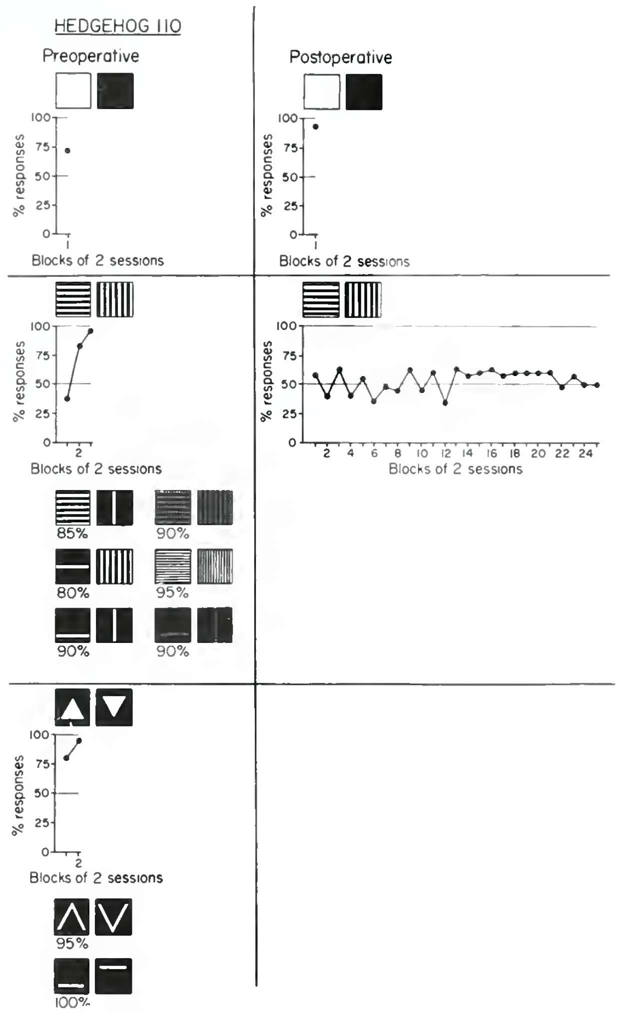
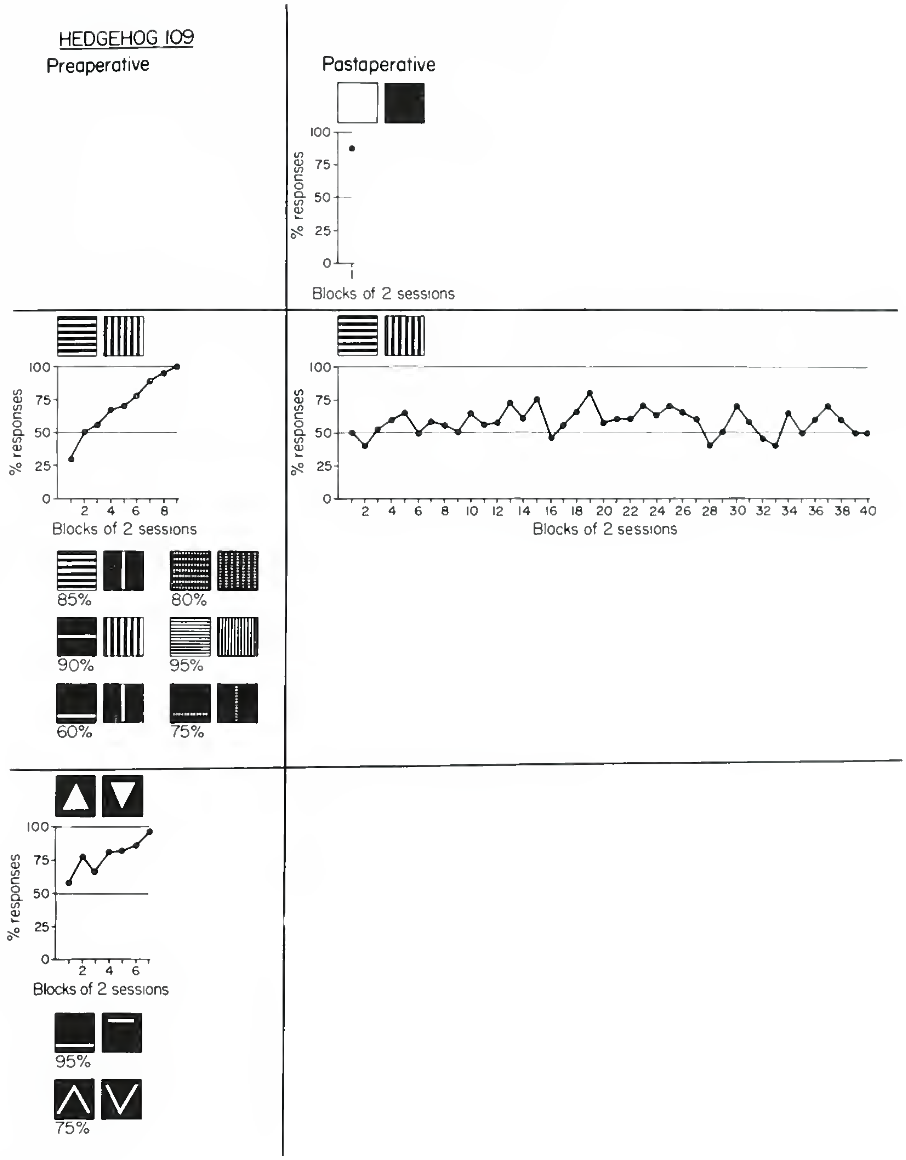

HEDGEHOG 110
Preoperative
Postoperative
% responses
Blocks of 2 sessions
85%
90%
80%
95%
90%
90%
95%
100%

Figure 34. Behavioral Results for Hedgehog 109. After 80 postoperative sessions, Hedgehog 109 was still performing at a chance level on the horizontal versus vertical stripes discrimination. Since the animal failed to relearn the stripes discrimination there was no postoperative training to the triangle problem. Preoperatively, there was no training to the light versus no-light task.


HEDGEHOG 109
Preaperative
Postaperative
% responses
Blocks of 2 sessions
85%
80%
90%
95%
60%
75%
95%
75%

after eighty sessions (Fig. 34). In contrast, all of the animals in the first group were able to attain a level of performance well above chance in much fewer than fifty sessions.

Cortical Lesions and Thalamic Degeneration

The reconstructions of the lesions and thalamic degeneration for the ten animals are presented in Figures 35 to 54. It is immediately apparent that lesion size is not the critical factor responsible for the difference between the two groups. Thus, of the seven animals which relearned, all but two, Hedgehogs 46 and 44, had bilateral lesions at least as extensive as the ablation in Hedgehog 110, an animal which failed to relearn (Figs. 35 to 38, 51-52). Furthermore, in two of the animals, Hedgehogs 21 and 41, the lesions extended from the midline to the rhinal sulcus, removing considerably more cortex than even the most extensive ablations in the second group (Figs. 45 to 48). Although retarded with respect to normal hedgehogs, both of these animals were able to maintain a relatively high level of performance.

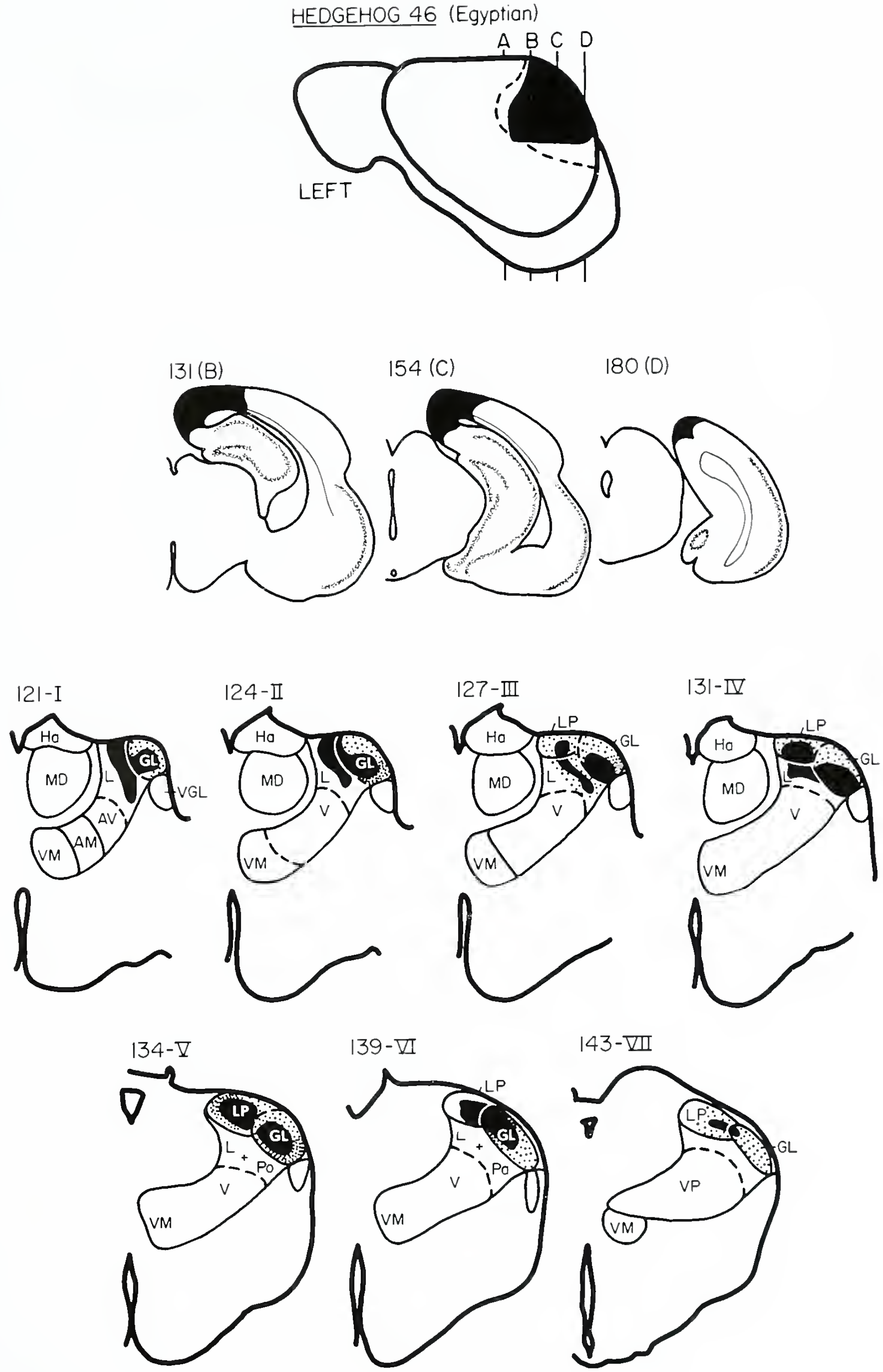
The results obtained in the retrograde degeneration experiments provide a basis for relating the cortical areas

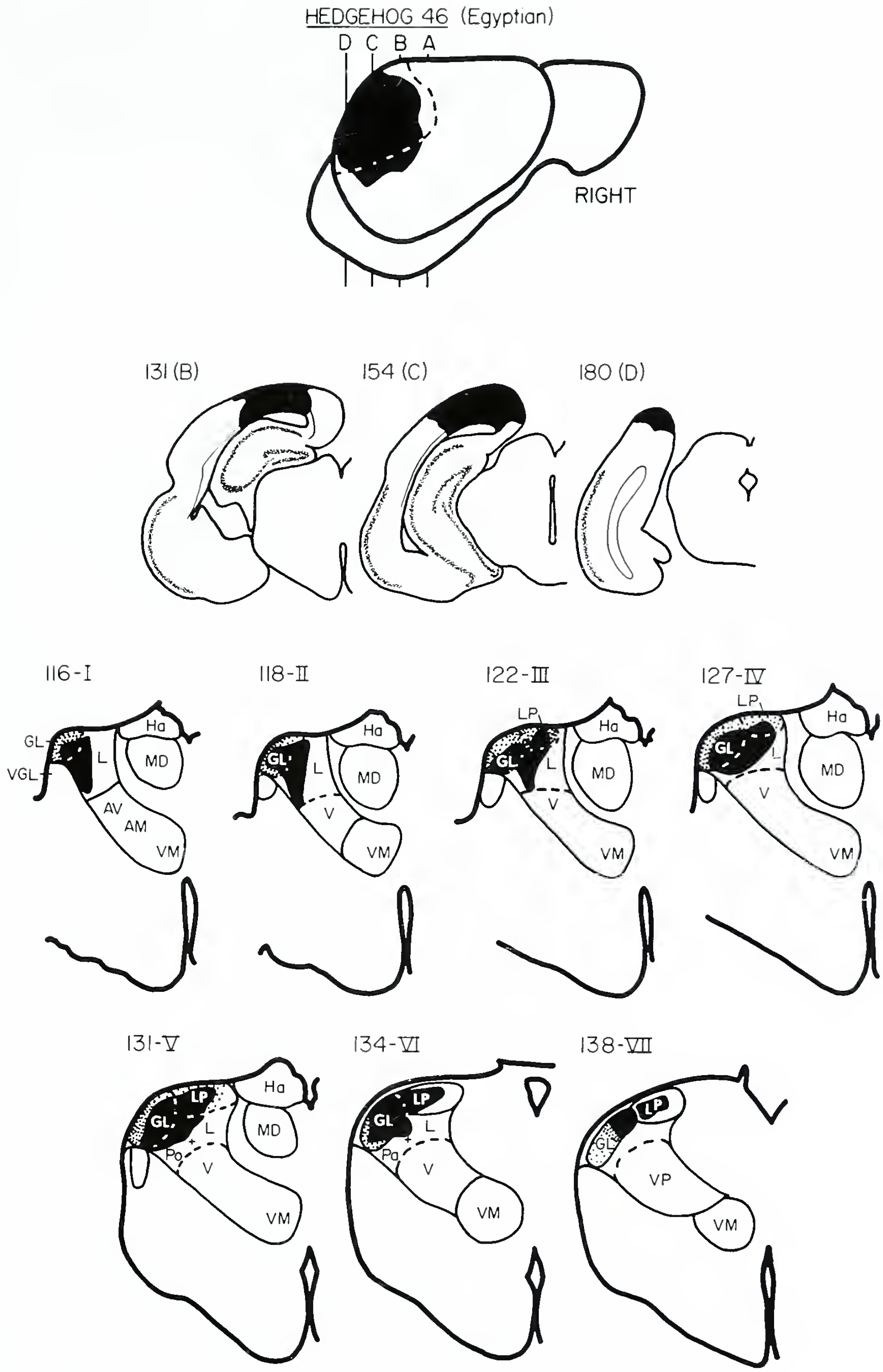
removed to the projection of the lateral geniculate. Thus, in the cases with large lesions which still relearned, for example, Hedgehogs 29, 43, 47, 21 and 41, not only was the total amount of cortex ablated extensive, but the areas removed are known to be the projection targets of the lateral geniculate (Figs. 39 to 48). Predictably, therefore, large portions of the lateral geniculate were severely degenerated. This expectation is realized by the extent of severe degeneration in each of the animals with large lesions. Indeed, the extent of severe degeneration in at least four of these animals, Hedgehogs 29, 43, 21 and 41, indicates that the lesions included more of the total projection target of the lateral geniculate than in the case of Hedgehog 110, an animal which did not relearn (Figs. 39 to 42, 45 to 48, 51-52). In two of these four, Hedgehogs 21 and 41, the lateral geniculates were severely degenerated except for small portions of the posterior tip whereas only moderate degeneration was present throughout the same sectors in Hedgehog 48, the animal with the largest lesion in the group which failed to relearn (Figs. 45 to 50). In the remaining two cases which failed to relearn, Hedgehogs 110 and 109, even larger proportions of the lateral geniculate underwent only moderate degeneration (Figs. 51 to 54). These cases indicate that neither lesion size nor severity of degeneration can account for the behavioral differences between the two groups.

The critical anatomical subdivision for distinguishing between the two groups is the visual area as defined by cytoarchitectonics. All seven of the animals which relearned had lesions which spared at least a small segment of this cortical region. In two of the animals, Hedgehogs 46 and 44, the lesions were restricted primarily to the cytoarchitectonic visual area and cortex medial to it (Figs. 35 to 38). In both cases, however, cortex in the cytoarchitectonic visual area was spared bilaterally. The lesion in Hedgehog 29 (Figs. 39-40) differed from the previous two primarily by extending further laterally in each hemisphere; but as in the preceding two cases, a considerable amount of visual area was spared anteriorly and medially on both sides. The lesions in the remaining four cases, Hedgehogs 43, 47, 21 and 41 were similar (Figs. 41 to 48). In each of these animals cytoarchitectonically defined visual cortex was spared despite the extensive ablation of the surrounding cortical regions.

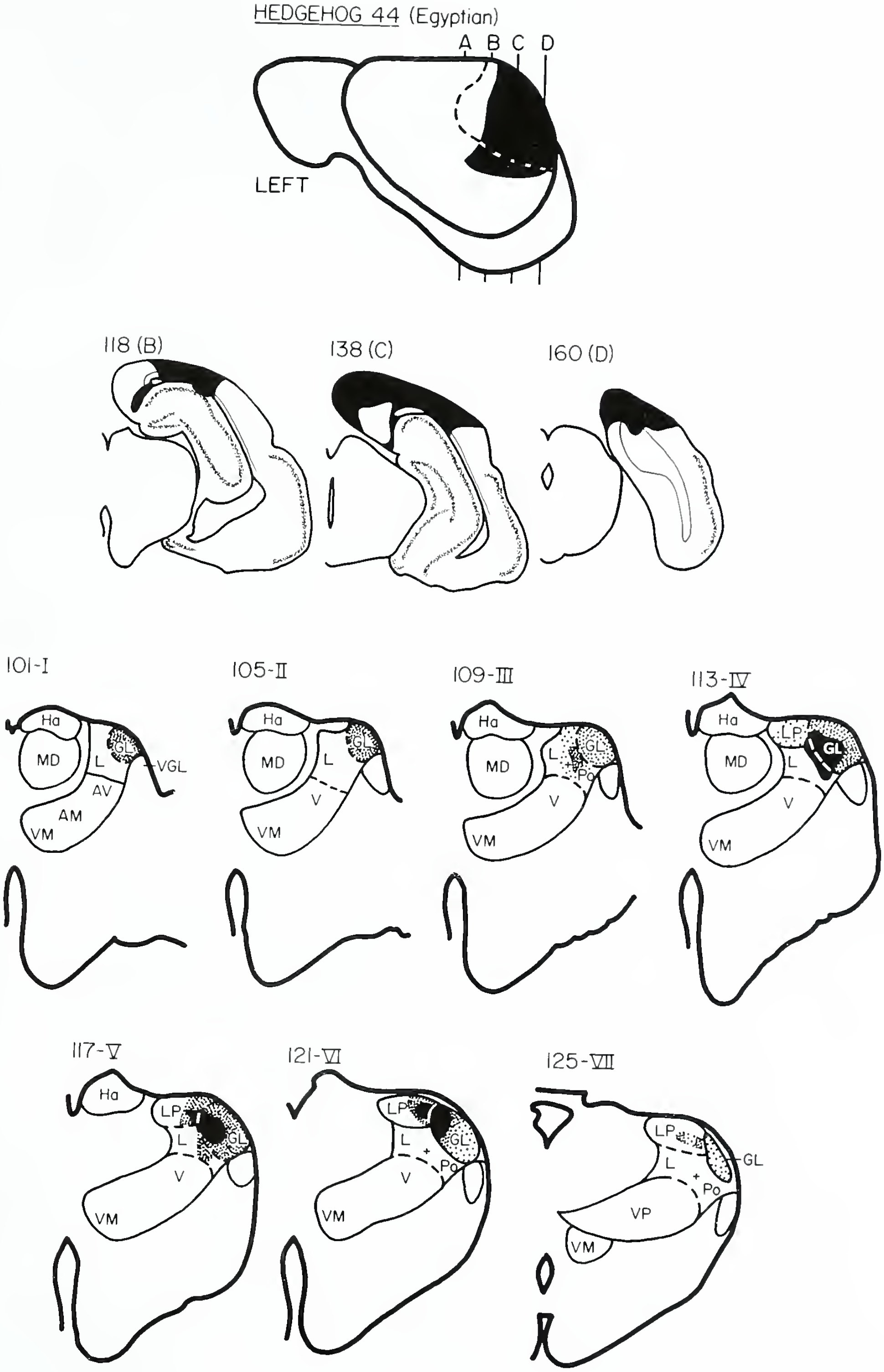
In contrast, the three animals which failed to relearn had complete ablations of visual cortex as defined by cytoarchitecture. The lesion in Hedgehog 48, the largest in this group, included on each side a considerable amount of cortex laterally in addition to the visual area (Figs. 49-50). On the other hand, the lesions in Cases 110 and 109 were more

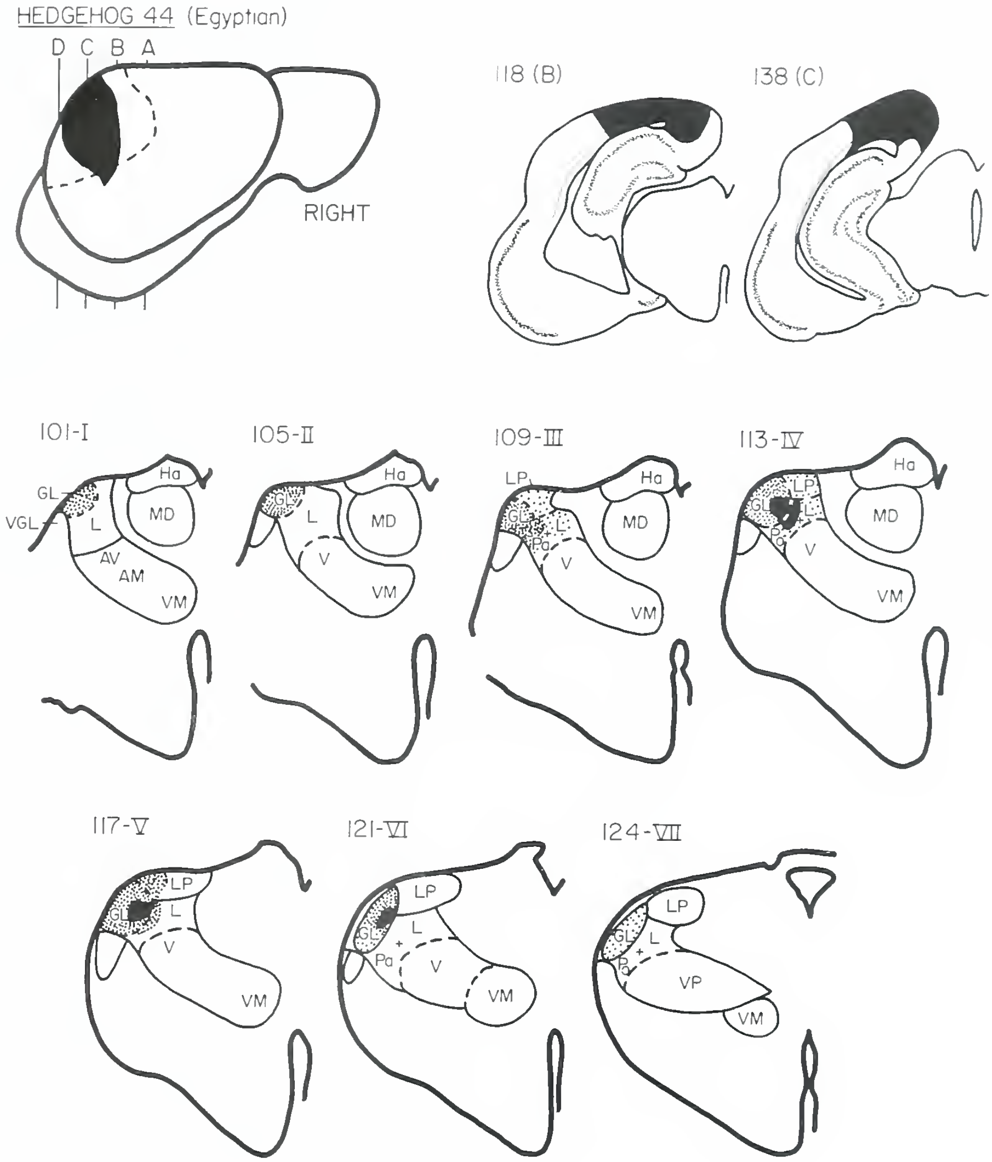
Figures 35 and 36. Cortical Lesion and Thalamic Degeneration in Hedgehog 46. The lesion in this animal is confined primarily to the cytoarchitectonic visual area and cortex medial to it. Portions of the visual area are, however, spared bilaterally. The degeneration in the lateral geniculate corresponds to the locus of the lesion; where the visual area is spared the corresponding part of the lateral geniculate is only slightly degenerated.


HEDGEHOG 46 (Egyptian)
A B C D
LEFT
131 (B)
154 (C)
180 (D)
121-I
124-II
127-III
131-IV
Ha
MD
L
GL
VGL
AV
AM
VM
V
LP
134-V
139-VI
143-VII
Po
VP


HEDGEHOG 46 (Egyptian)
D C B A
RIGHT
131 (B)
154 (C)
180 (D)
116-I
118-II
122-III
127-IV
GL
VGL
L
Ha
MD
AV
AM
VM
LP
V
131-V
134-VI
138-VII
Pa
VP

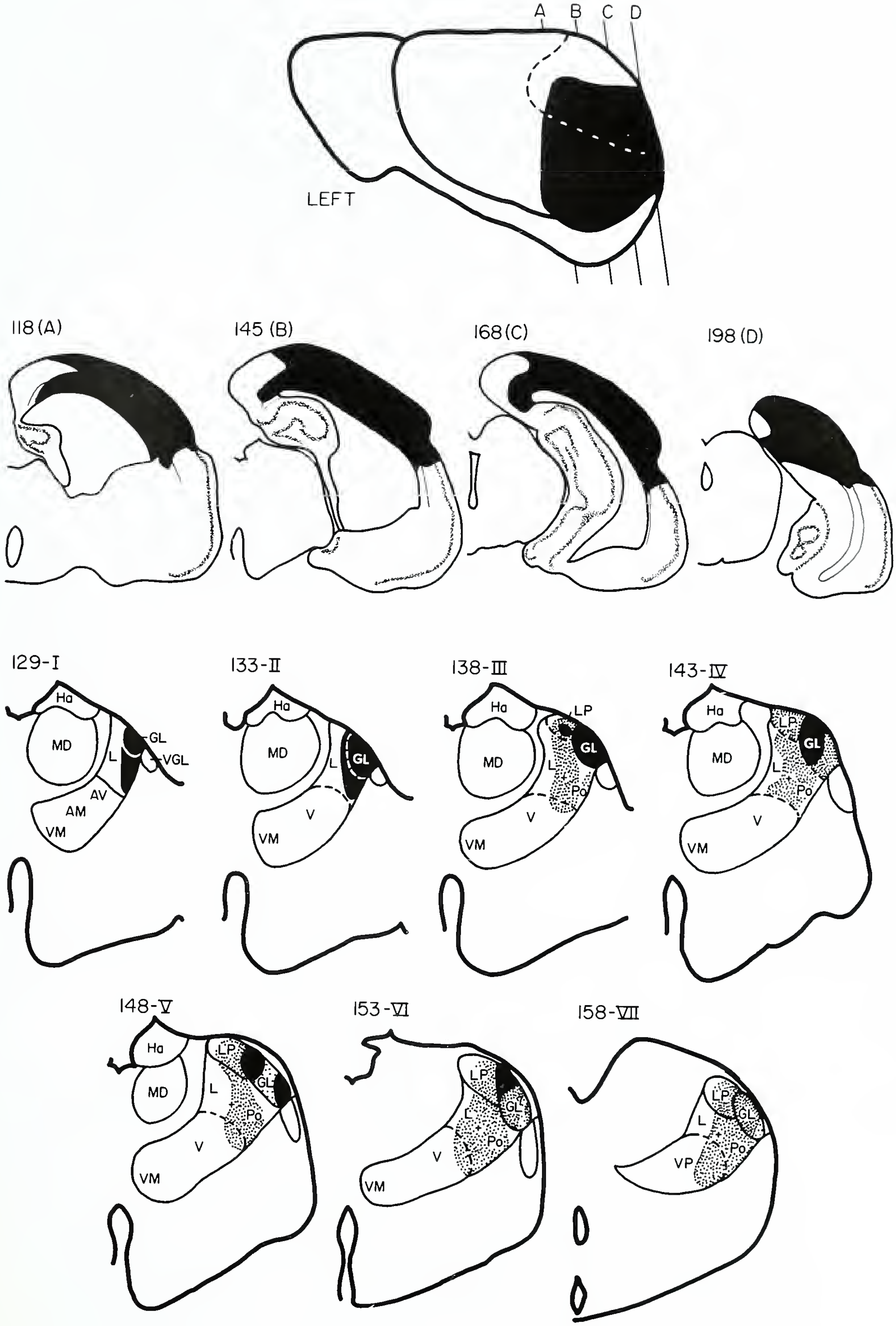
Figures 37 and 38. Cortical Lesion and Thalamic Degeneration in Hedgehog 44. Bilaterally, the lesions are restricted primarily to the cytoarchitectonic visual area. On each side, the lesion spares an anterior segment of the visual area and the posterior levels of both lateral geniculates contain regions of slight degeneration. The surface reconstruction of the lesion in the right hemisphere suggests that a posterior portion of the visual area is also spared on this side, but the presence of moderate rather than slight degeneration in anterior GL indicates that most of this region was undercut.

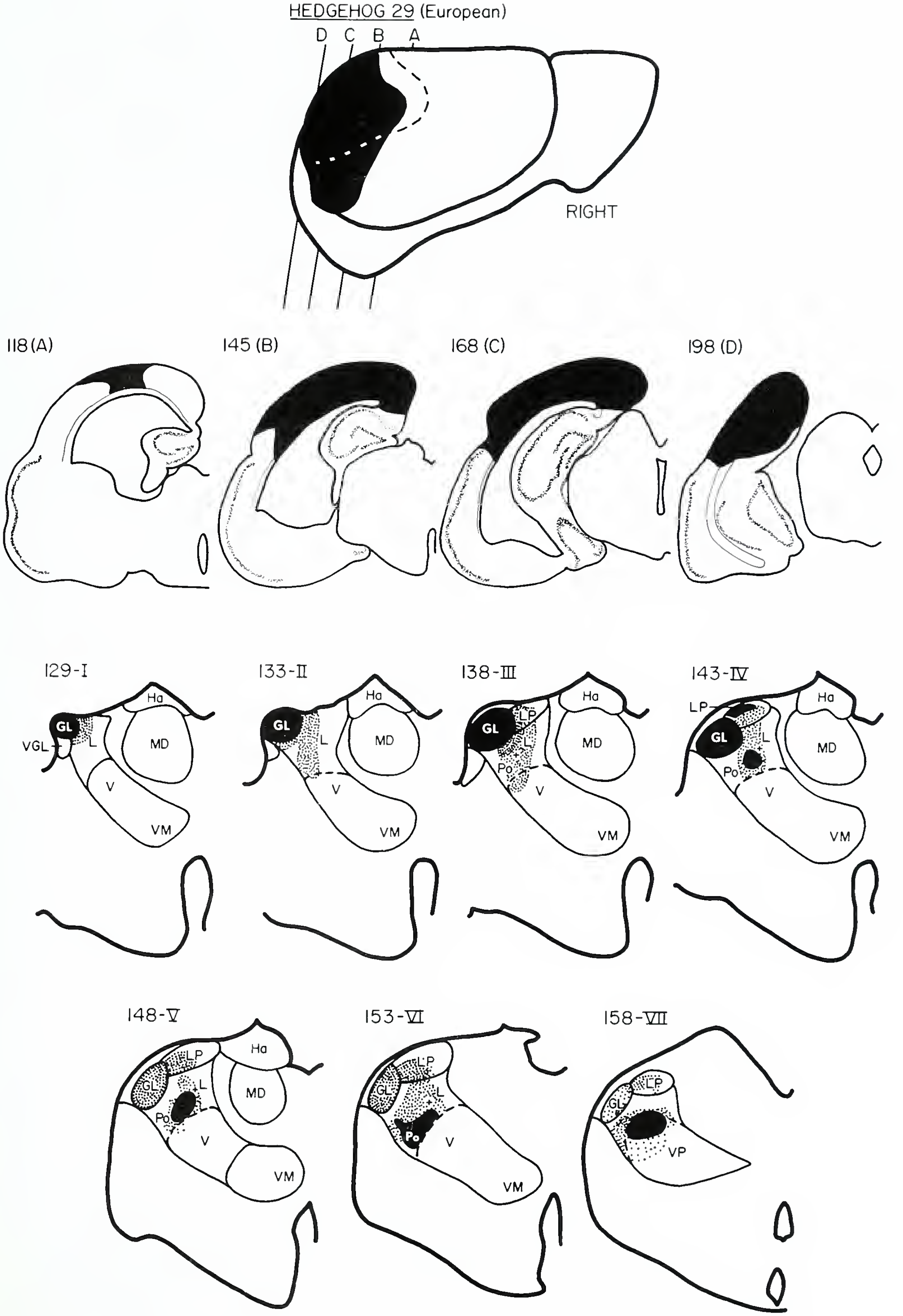

HEDGEHOG 44 (Egyptian)
A B C D
LEFT
118 (B)
138 (C)
160 (D)
101-I
Ha
MD
L
GL
VGL
AV
AM
VM
105-II
Ha
MD
L
GL
V
VM
109-III
Ha
MD
L
GL
Po
V
VM
113-IV
Ha
LP
MD
L
GL
V
VM
117-V
Ha
LP
L
GL
V
VM
121-VI
LP
L
GL
Po
V
VM
125-VII
LP
L
GL
Po
VP
VM


HEDGEHOG 44 (Egyptian)
D C B A
RIGHT
118 (B)
138 (C)
101-I
GL
VGL
L
Ha
MD
AV
AM
VM
105-II
L
Ha
MD
V
VM
109-III
LP
GL
L
Pa
Ha
MD
V
VM
113-IV
LP
GL
L
Pa
Ha
MD
V
VM
117-V
LP
GL
L
V
VM
121-VI
LP
GL
L
Pa
V
VM
124-VII
LP
GL
L
Pa
VP
VM

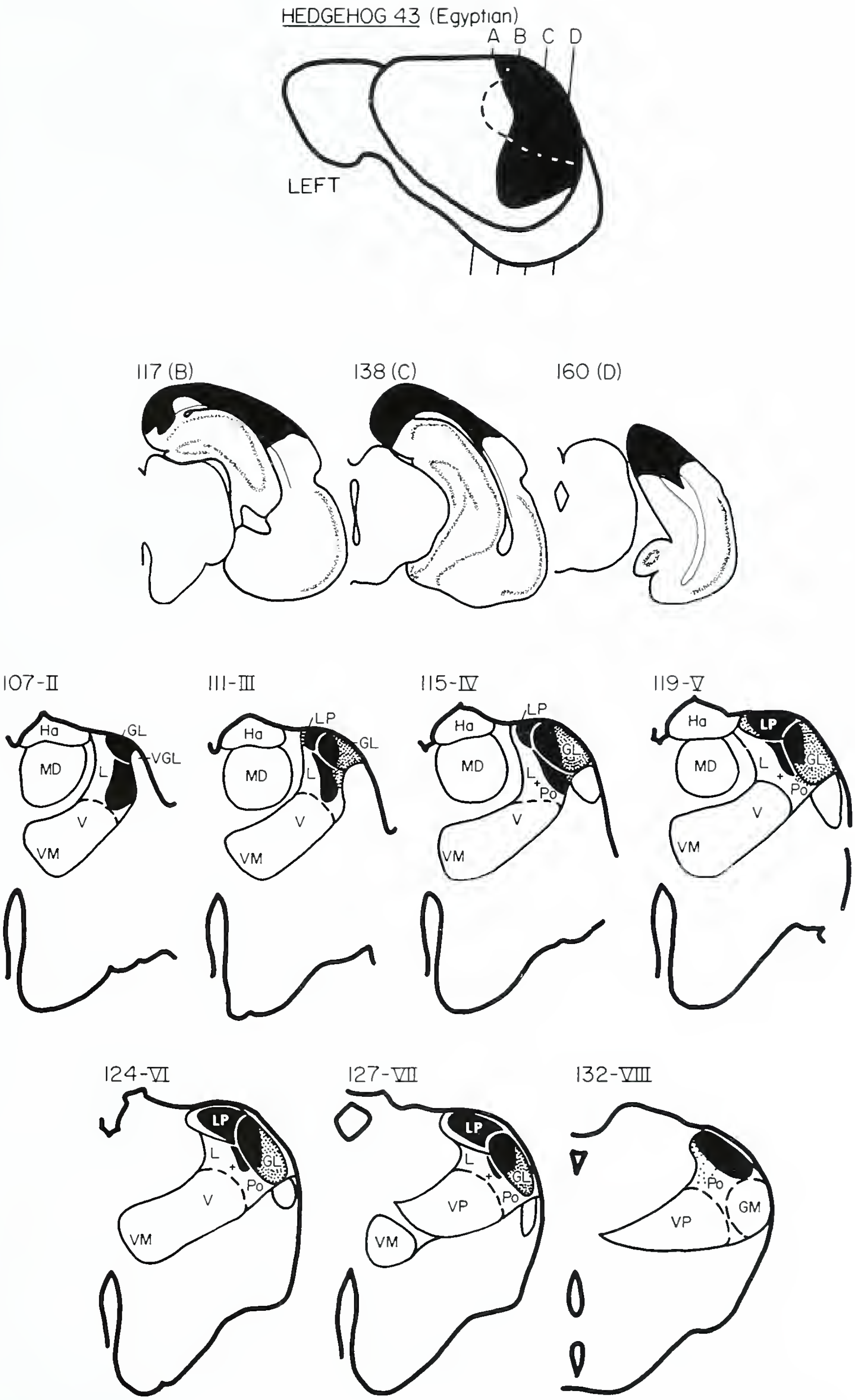
Figures 39 and 40. Cortical Lesion and Thalamic Degeneration in Hedgehog 29. The lesions in this animal extend laterally in each hemisphere to include large amounts of the cortex surrounding the cytoarchitectonic visual area. On the other hand, a considerable amount of visual area is spared on each side. The degeneration is severe in the anterior sectors of GL which project to posterior cortex. Posteriorly in GL, the degeneration is less severe reflecting in part the survival of anteromedial portions of the visual area.

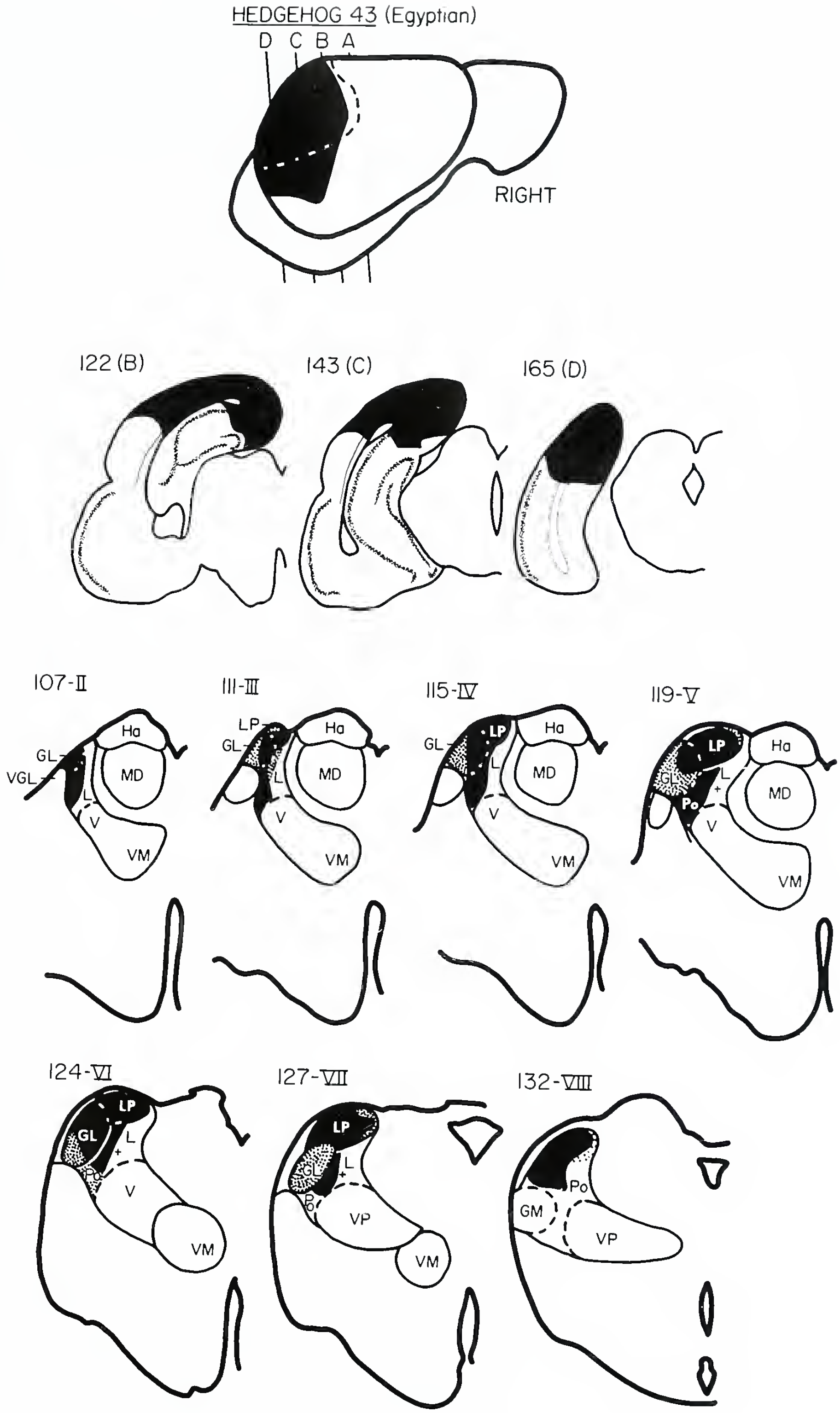
HEDGEHOG 29 (Europeon)




HEDGEHOG 29 (European)
D C B A
RIGHT
118 (A)
145 (B)
168 (C)
198 (D)
129-I
133-II
138-III
143-IV
148-V
153-VI
158-VII
GL
VGL
L
LP
Po
Ha
MD
V
VM
VP

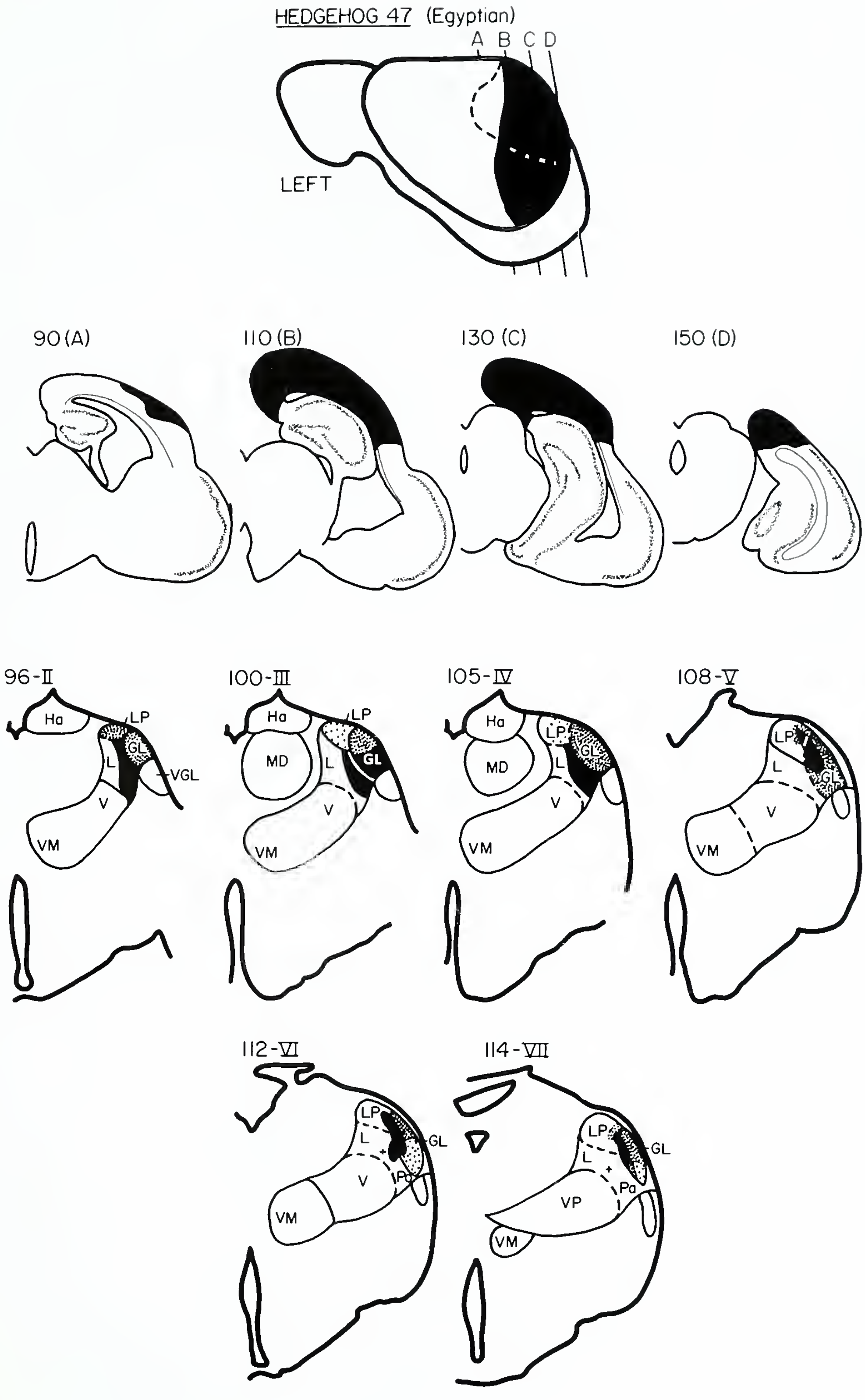
Figures 41 and 42. Cortical Lesion and Thalamic Degeneration in Hedgehog 43. The cortical lesions in this animal spare a portion of the cytoarchitectonic visual area while at the same time extending laterally to include large amounts of the surrounding cortex. Anterior GL is severely degenerated. Proceeding posteriorly in GL, the degeneration is less severe but never only slight, reflecting the fact that, although the anterior part of the visual area is spared, the cortex lateral and medial to it have been almost completely ablated.

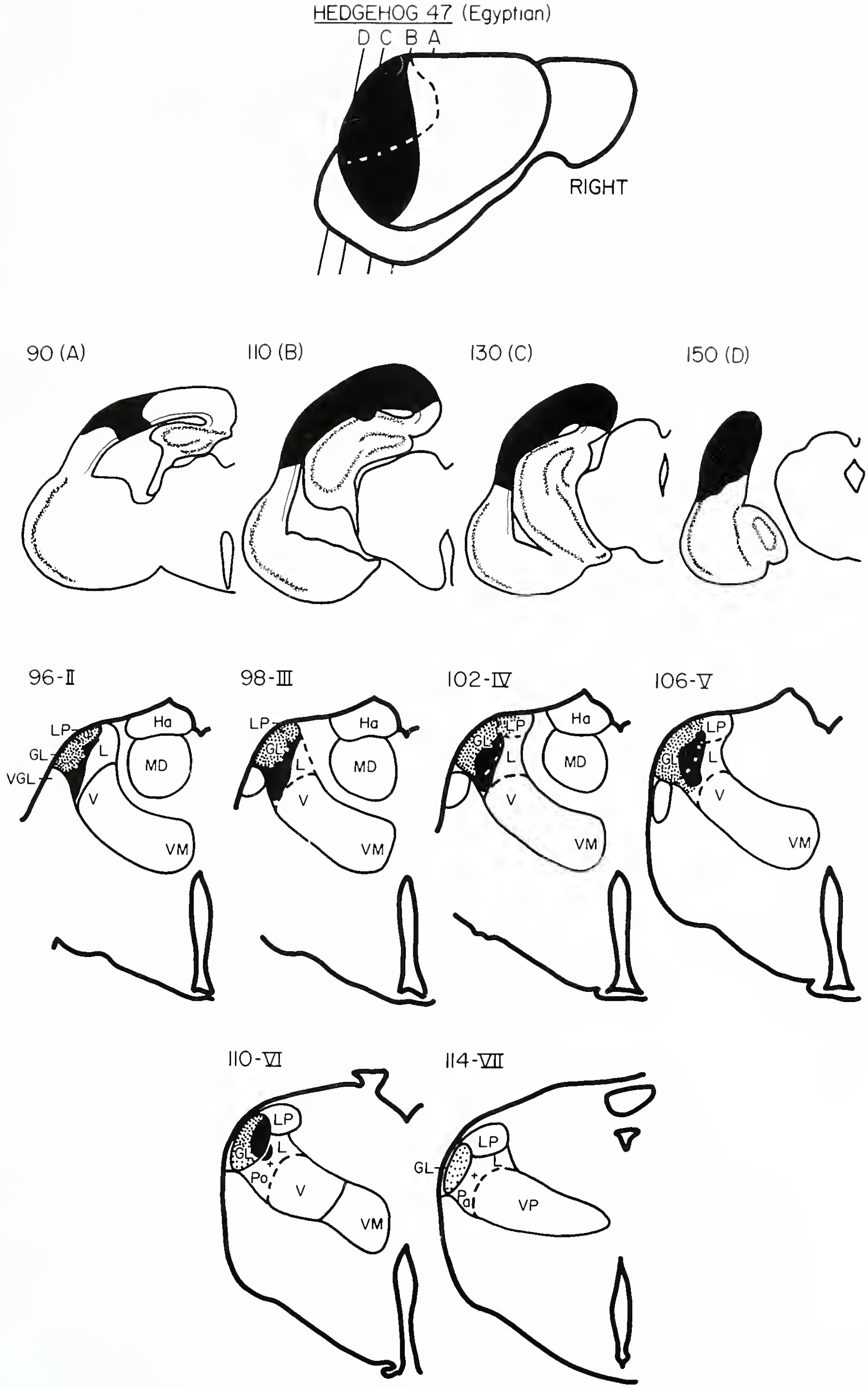

HEDGEHOG 43 (Egyptian)
A B C D
LEFT
117 (B)
138 (C)
160 (D)
107-II
Ha
GL
VGL
MD
L
V
VM
111-III
LP
GL
Ha
MD
L
V
VM
115-IV
LP
Ha
GL
MD
L
Po
V
VM
119-V
Ha
LP
MD
L
GL
Po
V
VM
124-VI
LP
L
GL
Po
V
VM
127-VII
LP
L
GL
Po
VP
VM
132-VIII
Po
GM
VP



HEDGEHOG 43 (Egyptian)
D C B A
RIGHT
122 (B)
143 (C)
165 (D)
107-II
GL
VGL
Ha
MD
L
V
VM
111-III
LP
GL
Ha
MD
L
V
VM
115-IV
GL
LP
Ha
MD
L
V
VM
119-V
LP
Ha
GL
Po
L
MD
V
VM
124-VI
LP
GL
L
Po
V
VM
127-VII
LP
GL
L
Po
VP
VM
132-VIII
Po
GM
VP

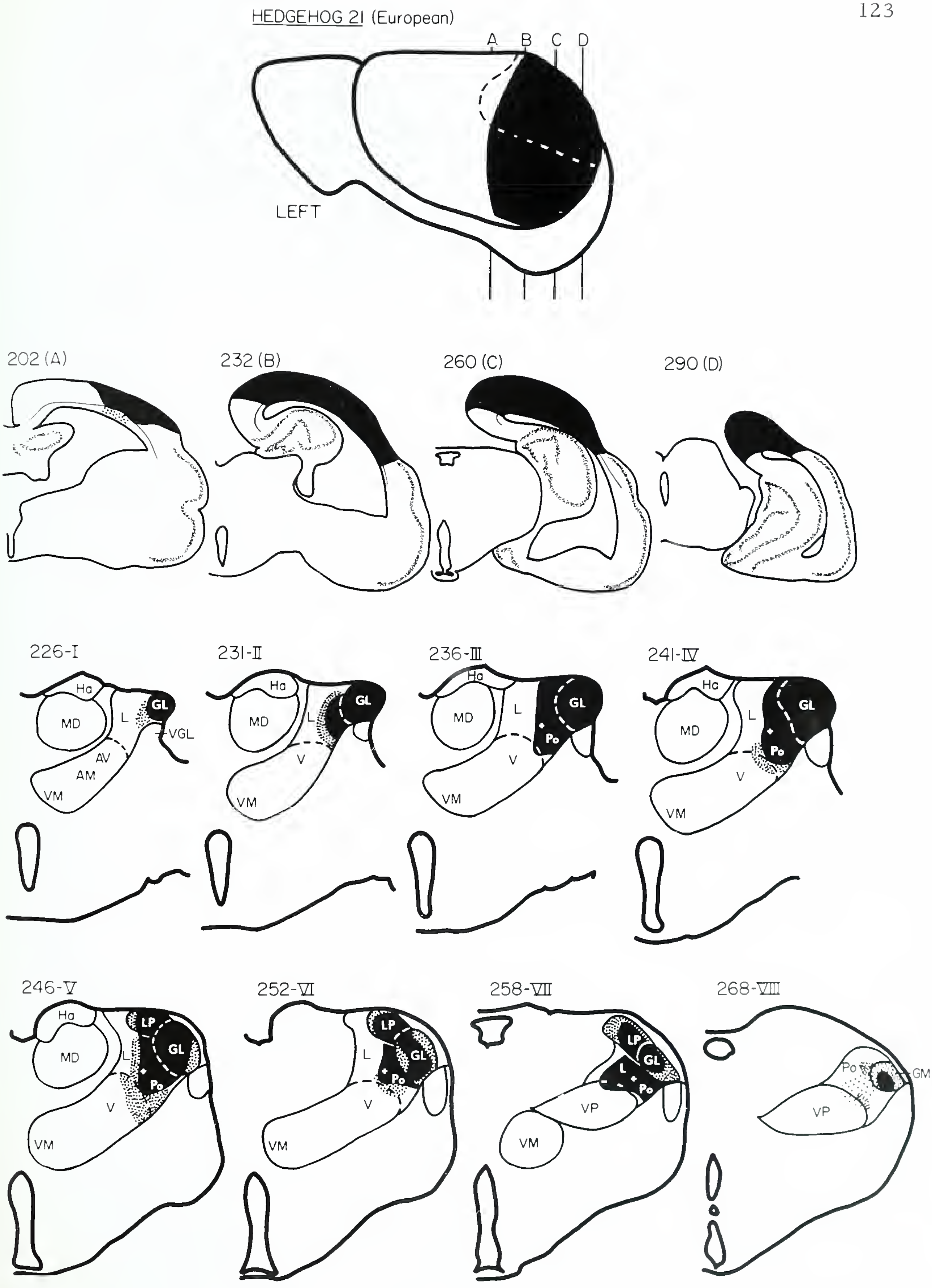
Figures 43 and 44. Cortical Lesion and Thalamic Degeneration in Hedgehog 47. The lesions extend from the medial wall to the rhinal sulcus posteriorly, but spare the anterior portion of the cytoarchitectonic visual area. Correspondingly, the degeneration is moderate to severe in anterior GL and becomes less severe in the more posterior levels.


HEDGEHOG 47 (Egyptian)
A B C D
LEFT
90 (A)
110 (B)
130 (C)
150 (D)
96-II
Ha
LP
GL
L
VGL
V
VM
100-III
Ha
LP
MD
L
GL
V
VM
105-IV
Ha
LP
MD
L
GL
V
VM
108-V
LP
L
GL
V
VM
112-VI
LP
L
GL
V
Pa
VM
114-VII
LP
L
GL
Pa
VP
VM

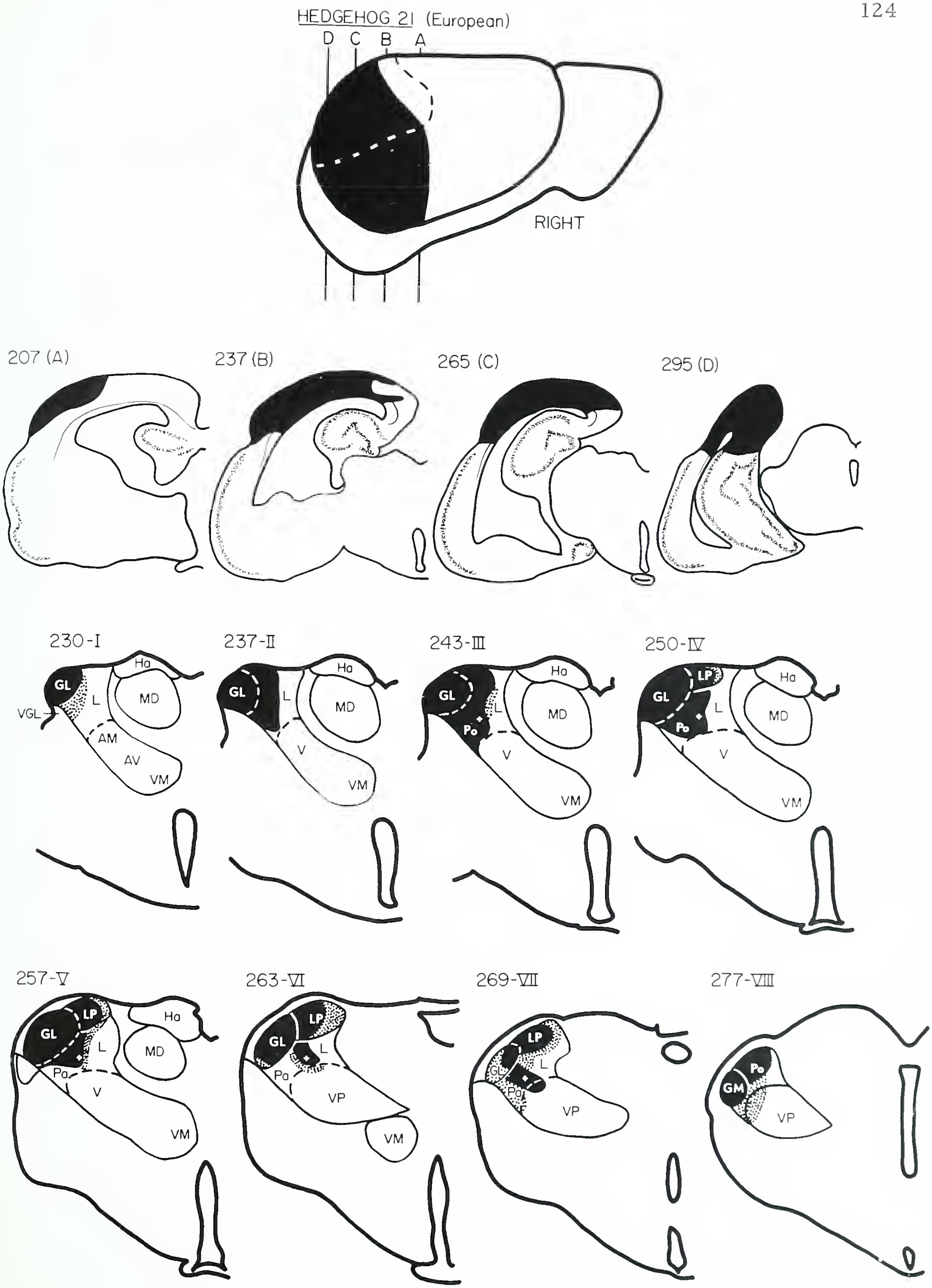


HEDGEHOG 47 (Egyptian)
D C B A
RIGHT
90 (A)
110 (B)
130 (C)
150 (D)
96-II
98-III
102-IV
106-V
LP
GL
VGL
L
V
Ha
MD
VM
110-VI
114-VII
Po
Pa
VP

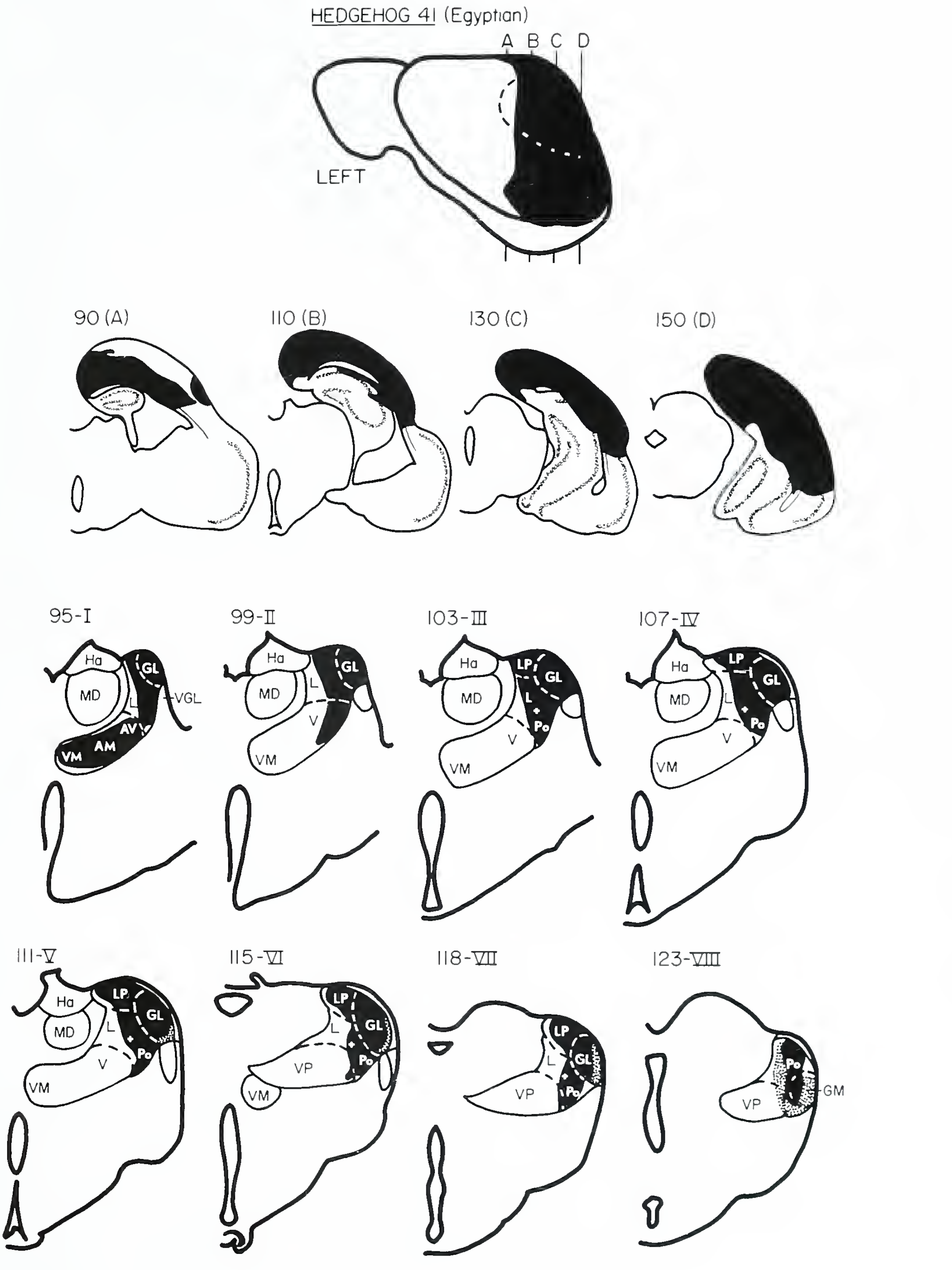
Figures 45 and 46. Cortical Lesion and Thalamic Degeneration in Hedgehog 21. Bilaterally, the lesion in Hedgehog 21 removes the posterior neocortex. On the other hand, on each side an anterior sector of the cytoarchitectonic visual area is spared. Correspondingly, anterior GL is severely degenerated whereas posterior GL is only moderately degenerated.

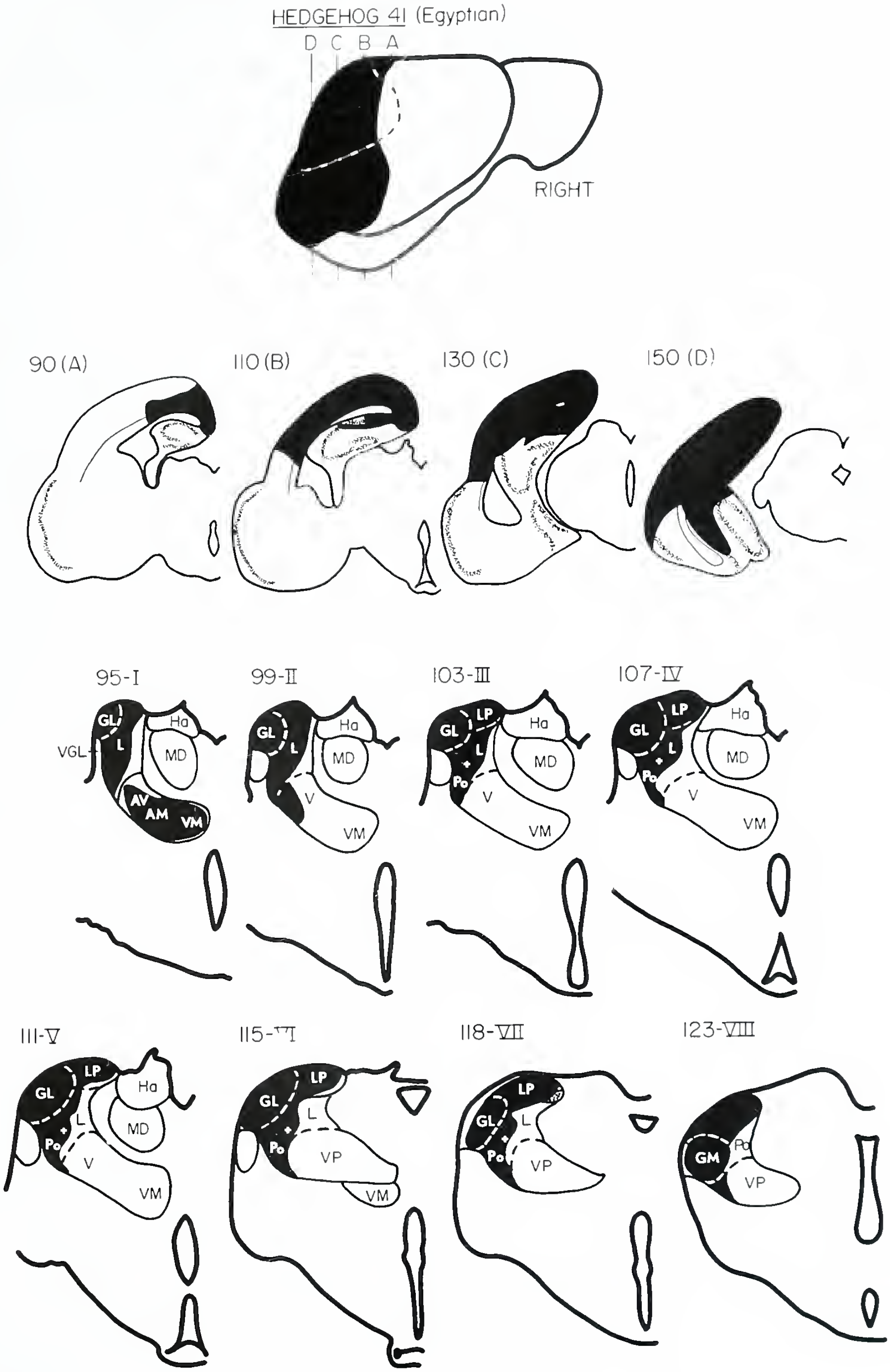


HEDGEHOG 21 (European)
A
B
C
D
LEFT
202 (A)
232 (B)
260 (C)
290 (D)
226-I
231-II
236-III
241-IV
Ha
MD
L
GL
VGL
AV
AM
VM
V
Po
246-V
252-VI
258-VII
268-VIII
LP
VP
GM

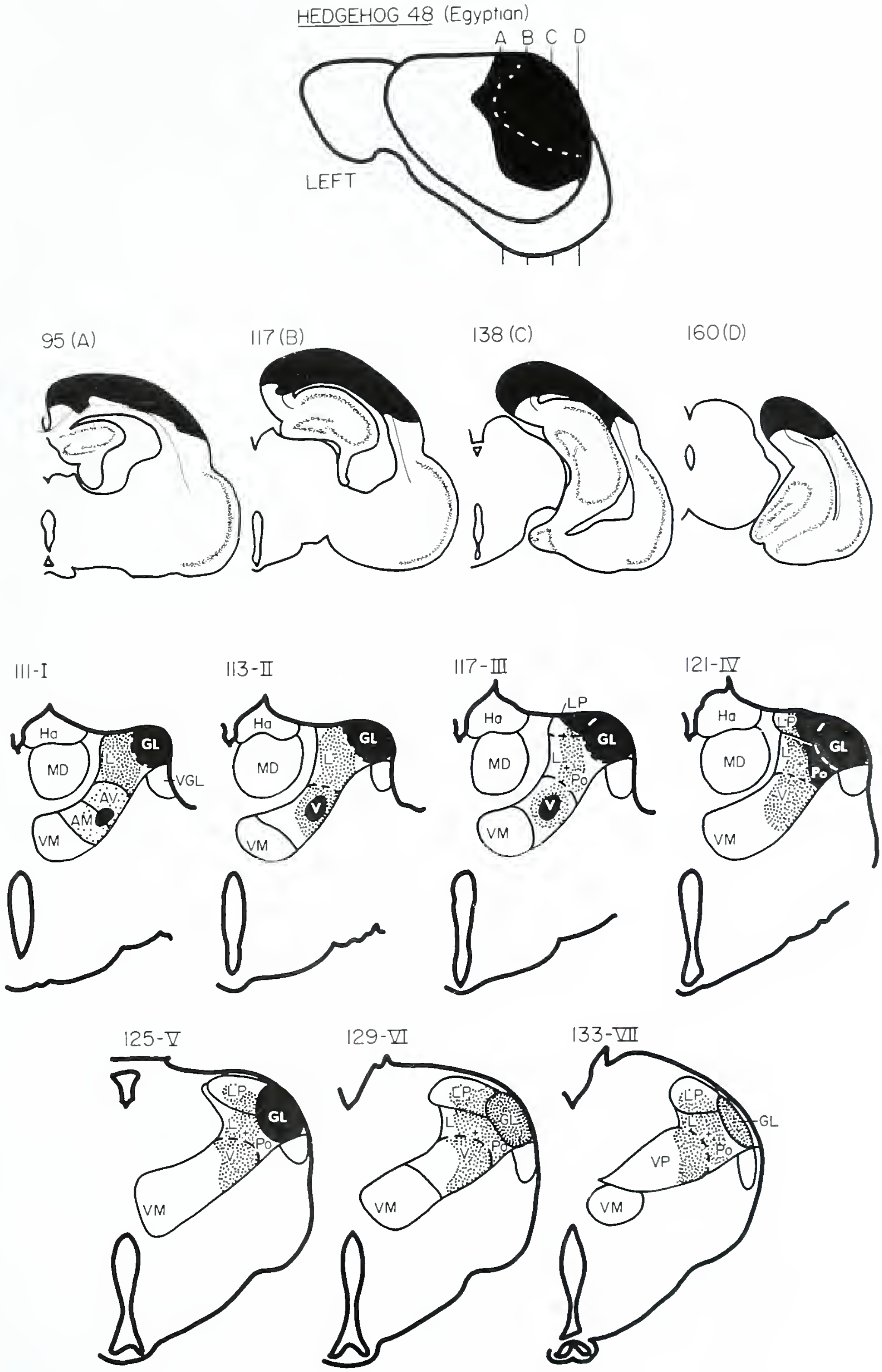

HEDGEHOG 21 (European)
D C B A
RIGHT
207 (A)
237 (B)
265 (C)
295 (D)
230-I
GL
VGL
L
Ha
MD
AM
AV
VM
237-II
GL
L
Ha
MD
V
VM
243-III
GL
Po
L
Ha
MD
V
VM
250-IV
LP
GL
Po
L
Ha
MD
V
VM
257-V
GL
LP
L
Ha
MD
Pa
V
VM
263-VI
LP
GL
L
Pa
VP
VM
269-VII
LP
GL
L
Pa
VP
277-VIII
Po
GM
VP

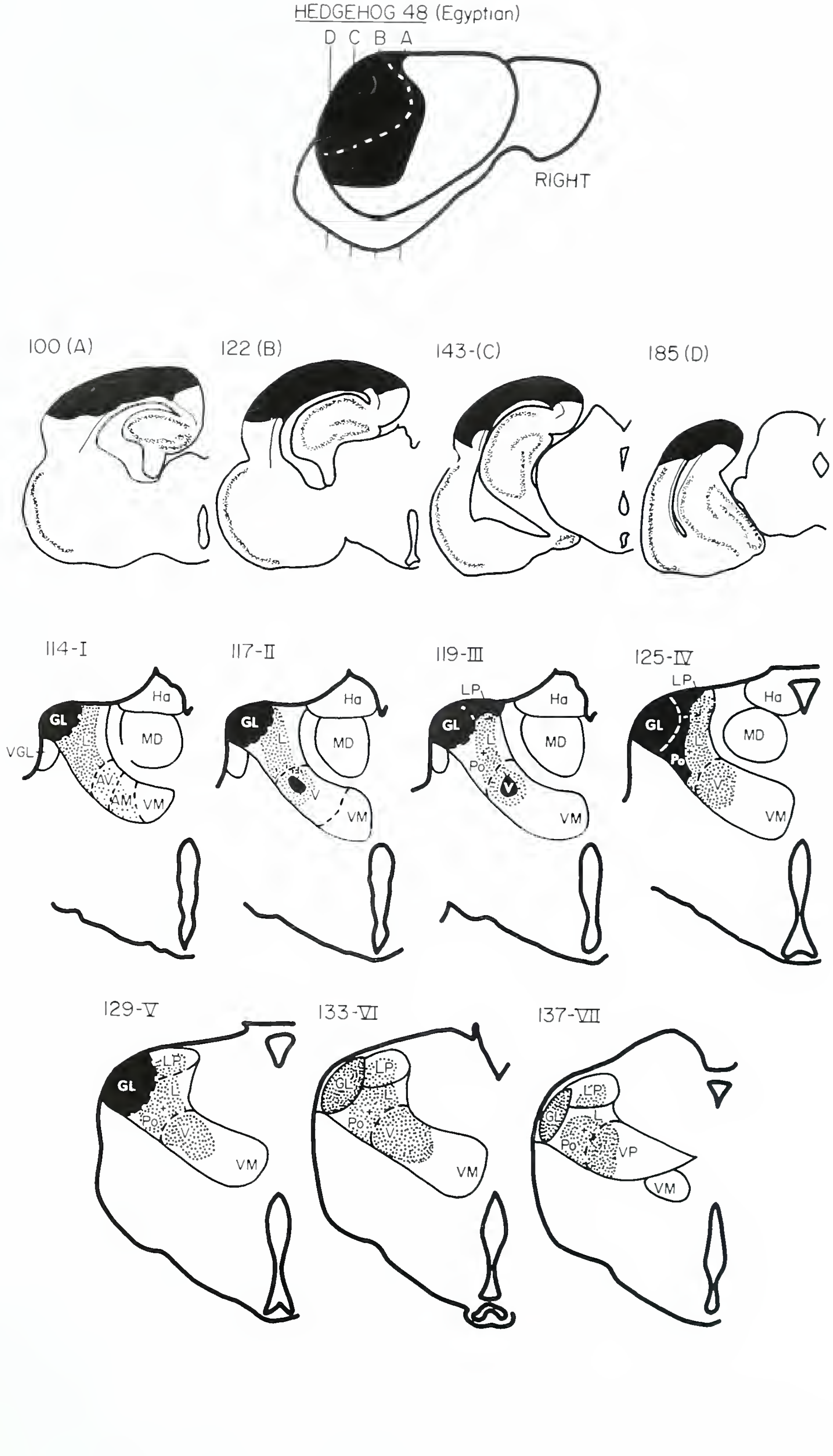
Figures 47 and 48. Cortical Lesion and Thalamic Degeneration in Hedgehog 41. On the left side, the ablation extends from the midline to the rhinal sulcus throughout most of the posterior cortex. A small segment of the cytoarchitectonic visual area remains anteriorly and in the left lateral geniculate a region of moderate degeneration is present in the posterior three levels. In the right hemisphere, the surface reconstruction of the lesion suggests that a portion of the visual area is also spared on this side, but, apparently due to undercutting of radiation fibers, GL is severely degenerated throughout.


HEDGEHOG 41 (Egyptian)
A B C D
LEFT
90 (A)
110 (B)
130 (C)
150 (D)
95-I
Ha
MD
GL
VGL
L
AV
AM
VM
99-II
V
103-III
LP
Po
107-IV
111-V
115-VI
VP
118-VII
123-VIII
GM

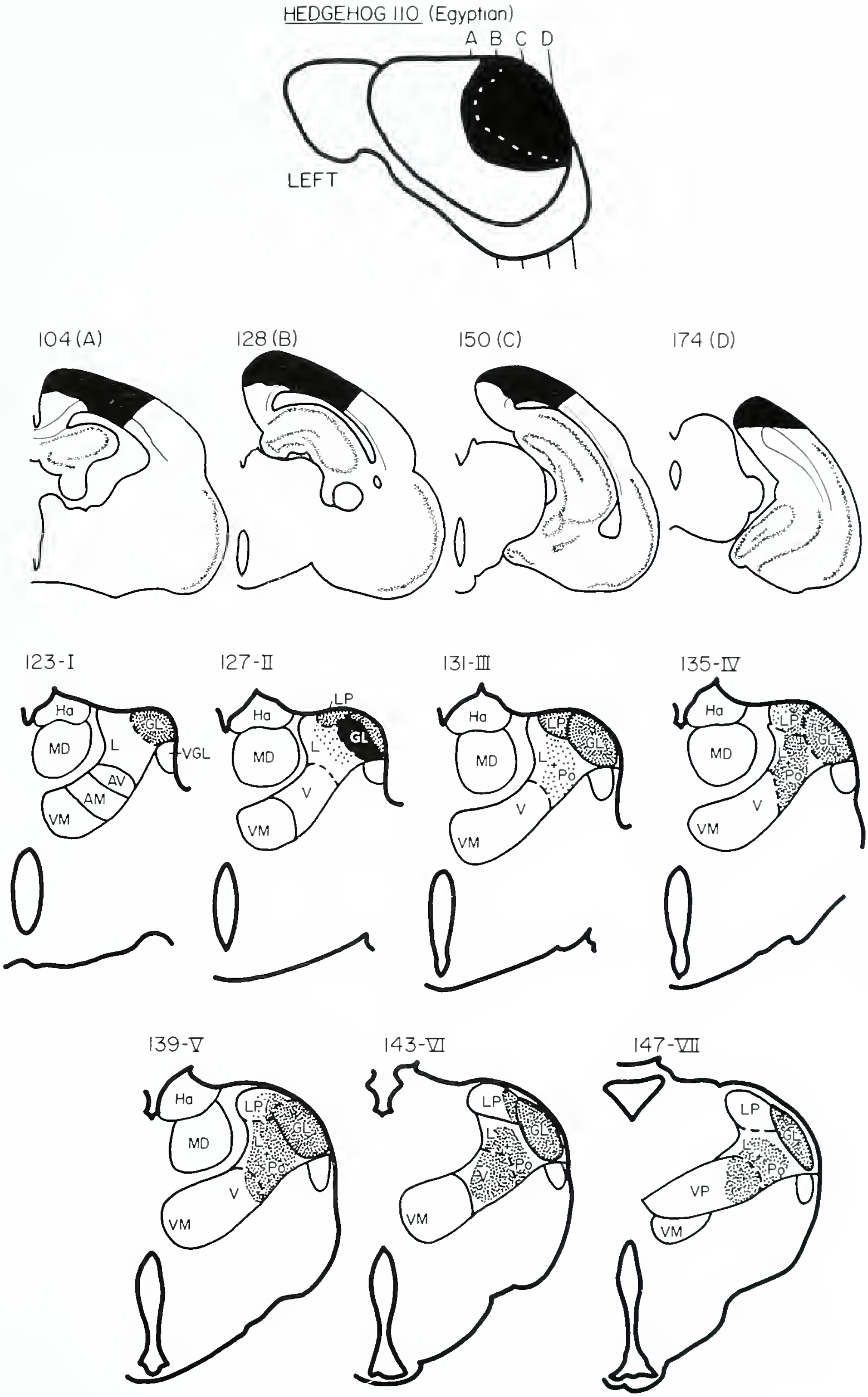

HEDGEHOG 41 (Egyptian)
D C B A
RIGHT
90 (A)
110 (B)
130 (C)
150 (D)
95-I
99-II
103-III
107-IV
GL
L
VGL
Ha
MD
AV
AM
VM
V
LP
Po
111-V
115-VI
118-VII
123-VIII
VP
GM

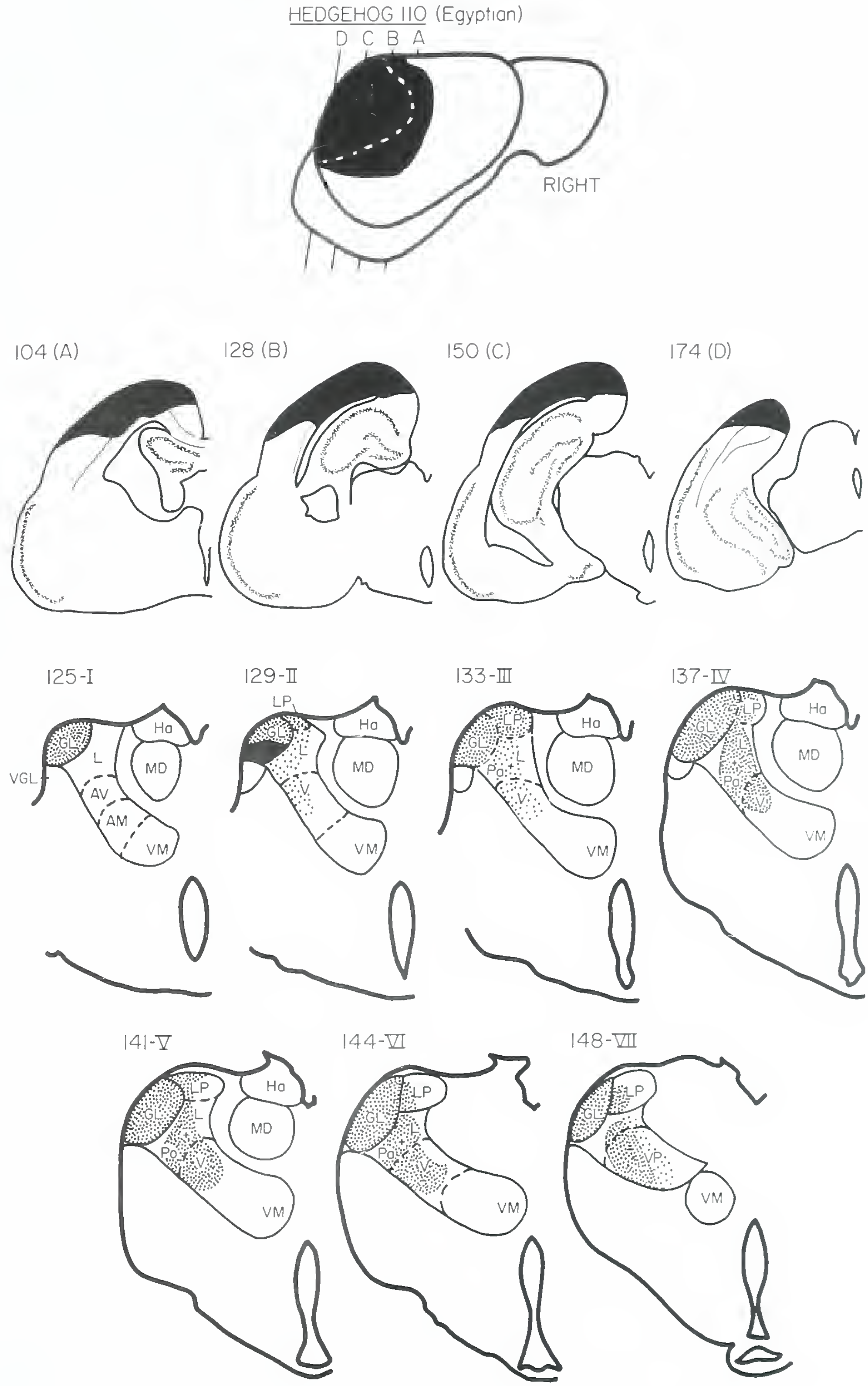
Figures 49 and 50. Cortical Lesion and Thalamic Degeneration in Hedgehog 48. The entire visual area as defined by cytoarchitecture is ablated in Hedgehog 48. On each side the lesion extends a considerable distance lateral to the posterior part of the visual area and the anterior levels of the lateral geniculates are severely degenerated. Anteriorly, the lesions spared most of the cortex surrounding the visual area and, correspondingly, many neurons remain in posterior GL.


HEDGEHOG 48 (Egyptian)
A B C D
LEFT
95 (A)
117 (B)
138 (C)
160 (D)
111-I
113-II
117-III
121-IV
Ha
MD
GL
L
VGL
AV
AM
VM
V
LP
Po
125-V
129-VI
133-VII
VP

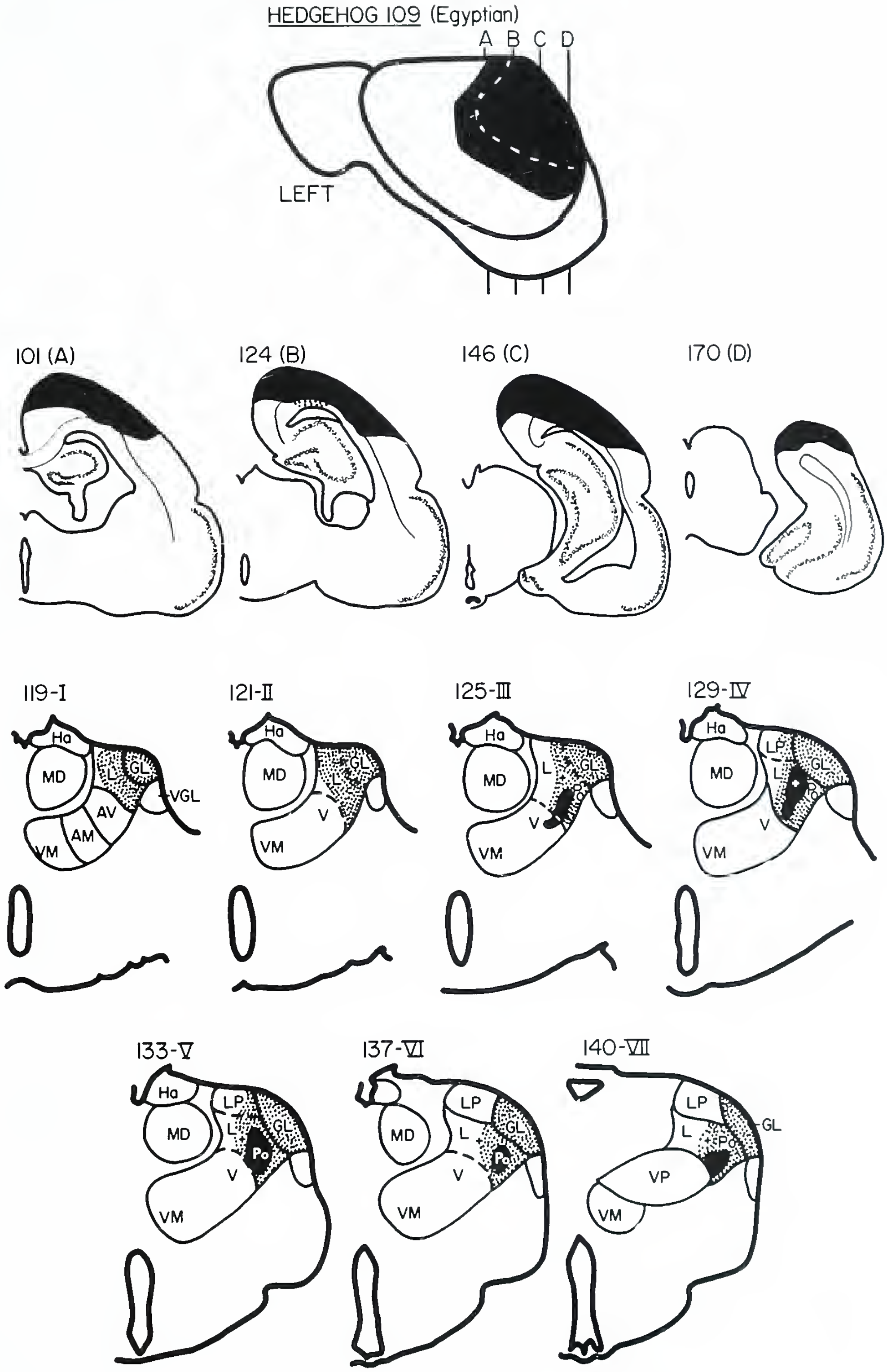

HEDGEHOG 48 (Egyptian)
D C B A
RIGHT
100 (A)
122 (B)
143-(C)
185 (D)
114-I
117-II
119-III
125-IV
Ha
GL
VGL
MD
L
AV
AM
VM
V
LP
Po
129-V
133-VI
137-VII
VP

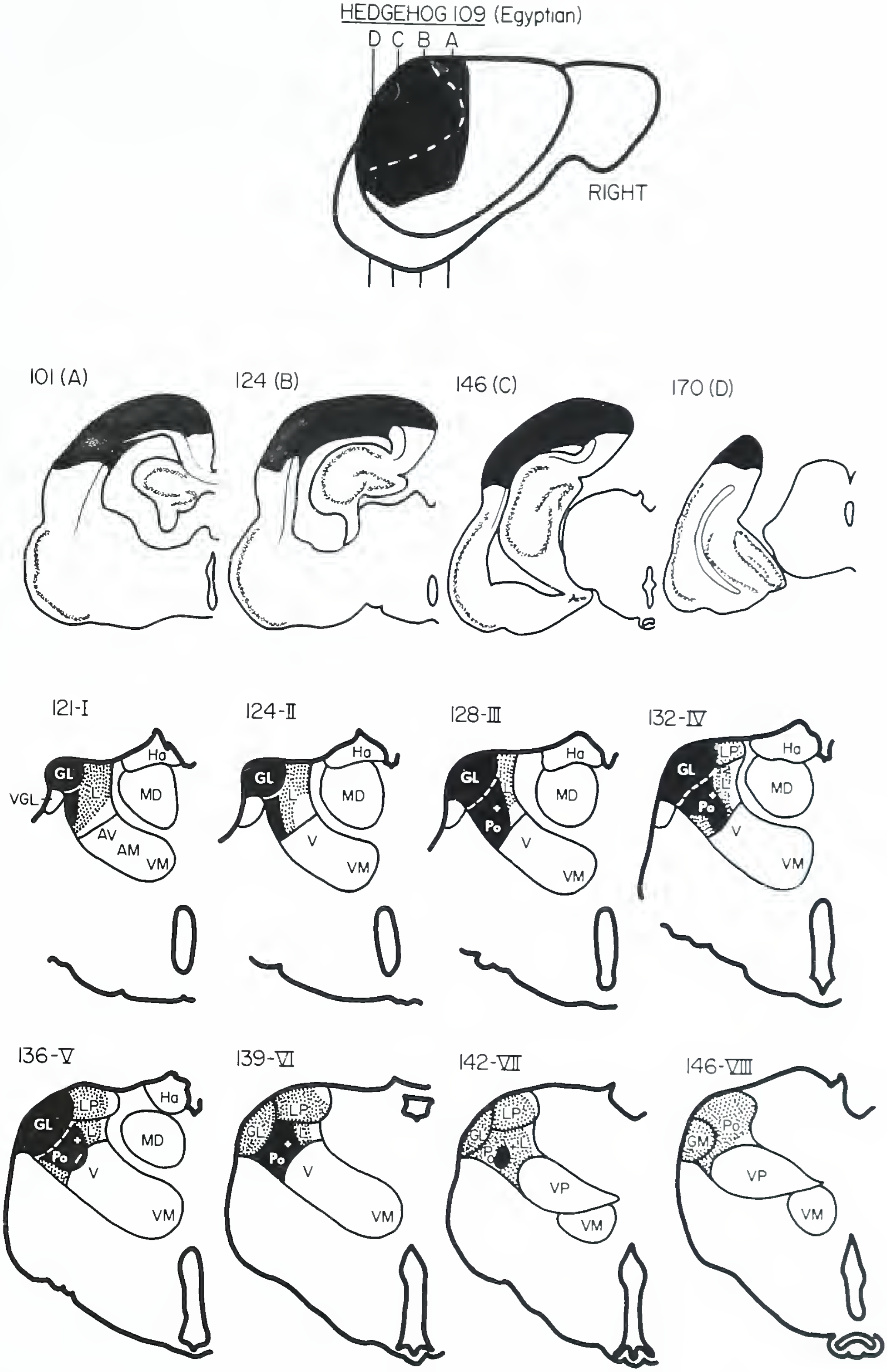
Figures 51 and 52. Cortical Lesion and Thalamic Degeneration in Hedgehog 110. The entire cytoarchitectonic visual area in Hedgehog 110 is removed. On the other hand, in each hemisphere the lesion spares considerable portions of the surrounding cortex. Throughout most of the lateral geniculate on each side many neurons remain confirming that portions of the projection target of this nucleus are intact.


HEDGEHOG 110 (Egyptian)
A B C D
LEFT
104 (A)
128 (B)
150 (C)
174 (D)
123-I
Ha
MD
L
GL
VGL
AV
AM
VM
127-II
Ha
LP
GL
MD
L
V
VM
131-III
Ha
LP
GL
MD
L
Po
V
VM
135-IV
Ha
LP
GL
MD
L
Po
V
VM
139-V
Ha
LP
GL
MD
L
Po
V
VM
143-VI
LP
GL
L
V
Po
VM
147-VII
LP
GL
L
Po
VP
VM


HEDGEHOG 110 (Egyptian)
D C B A
RIGHT
104 (A)
128 (B)
150 (C)
174 (D)
125-I
129-II
133-III
137-IV
141-V
144-VI
148-VII
GL
L
Ha
MD
VGL
AV
AM
VM
LP
V
Pa
VP

Figures 53 and 54. Cortical Lesion and Thalamic Degeneration in Hedgehog 109. The entire cytoarchitectonically defined visual area is removed in Hedgehog 109. On the left side, considerable amounts of cortex outside of the visual area are spared and the degeneration in the lateral geniculate is only moderate. On the right side the damage to cortical regions outside of the cytoarchitectonic visual area is more extensive and large portions of anterior GL are severely degenerated.


HEDGEHOG 109 (Egyptian)
A B C D
LEFT
101 (A)
124 (B)
146 (C)
170 (D)
119-I
Ha
MD
L
GL
VGL
AV
AM
VM
121-II
125-III
129-IV
LP
V
Po
133-V
137-VI
140-VII
VP


HEDGEHOG 109 (Egyptian)
D C B A
RIGHT
101 (A)
124 (B)
146 (C)
170 (D)
121-I
GL
VGL
L
Ha
MD
AV
AM
VM
124-II
128-III
Po
V
132-IV
LP
136-V
139-VI
142-VII
VP
146-VIII
GM

restricted (Figs. 51 to 54). Whereas in both animals the visual area defined in terms of cytoarchitecture was completely removed, extensive amounts of visual cortex as defined by the total projection target of the lateral geniculate was spared.

The Results of Equivalence Tests

In order to study in detail the basis for the discriminations made by the postoperative hedgehogs, an extensive series of equivalence tests was designed. These tests were administered following training to the stripe and triangle discriminations. Figure 55 illustrates each of these thirteen tests and summarizes the results obtained from normal and postoperative animals. The scores made by each animal on these tests are included in the Figures which present the individual learning records (Figs. 25 to 34, Pages 85 to 103).

Over-all, the results for the postoperative animals - despite the wide variations in the size of the lesions and the severity of the relearning deficits - were similar to those obtained from normal animals. On the tests which followed training to the stripe discrimination problem, the animals responded on the basis of the orientation of the lines both before and after surgery. For example, the single white line, the thin stripes, and the single row of white dots were

Figure 55. Chart of Equivalence Tests. All of the stimuli are drawn to scale. The Figure presents the percent of responses made by hedgehogs to the test stimuli before and after cortical surgery. Both the preoperative and postoperative scores are divided into subgroups according to the nature of the positive training stimulus. The pre-operative scores for the two and three choice situations are averaged since the results obtained were similar. In the three choice situation the animals received twelve presentations of each test; in the two choice situation, twenty presentations were given. All postoperative tests were given in the two choice situation. The scores obtained from each animal are presented in the Figures which illustrate the individual learning curves. With the exception of test D, the results for the individuals averaged in each group are consistent. Test D will be discussed in the text. The data for normal hedgehogs include the results from five animals which did not survive surgery.

A. Single 1/4 in. vertical and horizontal line. Each line bisects the stimulus card.
B. Single 1/4 in. lines with horizontal line low on stimulus card.
C. 1/8 in. horizontal and vertical stripes.
D. Rows of dots. The dots are 1/4 in. in diameter and are separated by 1/8 in.
E. Single row of dots. The size and spacing of the dots is the same as in test D.
F. Single 1/4 in. black lines on white background.
G. Single 1/4 in. vertical line and horizontal stripes.
H. Vertical stripes and single 1/4 in. horizontal line.
I. Similar to H except single horizontal line is low on stimulus card.
J. Vertical stripes and homogeneous white card.
K. Vertical stripes and homogeneous black card.
L. Triangle baselines. The baselines are 1/4 in. thick and 2.5 in. long.
M. Apical angles of triangles. The lines forming the angles are 1/4 in. thick.

TRAINING STIMULI	TESTS																					
Preoperative	91 (6)		77 (6)		92 (2)		95 (2)		65 (2)		57 (2)		80 (2)		77 (2)							
		62 (2)		75 (2)		92 (2)		85 (2)		82 (2)		54 (2)		85 (2)		85 (2)						
Postoperative	86 (4)		80 (4)		72 (4)		69 (4)		79 (4)		58 (3)		50 (4)		96 (4)				81 (4)		95 (4)	
		50 (2)		80 (1)		85 (1)		40 (1)				50 (2)		95 (2)		35 (2)		75 (1)				

Preoperative	80 (6)		56 (6)	
		86 (6)		62 (6)
Postoperative	75 (1)		70 (1)	
		100 (1)		65 (1)

found equivalent to the training stimulus by the majority of both the normal and postoperative animals regardless of whether vertical or horizontal was positive (tests A, C, E). On the other hand, neither the normal nor the postoperative group transferred from the positive training stimulus to the single black line on a white background (test F). While orientation was common to the stripe discrimination, regardless of which stimulus was positive, some interesting differences between animals were revealed depending on whether the vertical or the horizontal stripes were positive. A comparison of the results obtained from tests A and B indicates that both the pre- and postoperative animals trained to choose horizontal stripes tended subsequently to choose the single horizontal line only when it was low on the stimulus card. A similar tendency to respond to stimuli in the lower visual field has previously been reported for rats and also for monkeys (Lashley, 1938; Meyer, Treichler, and Meyer, 1965).

Since only two postoperative animals completed the triangle discrimination training, the equivalence tests which followed this task are not as interesting as those which were presented after the stripe discrimination. The results for tests L and M, however, indicate that, following training to triangles, both the normal and postoperative

animals tended to respond differentially to the baselines but not to the angles.

Despite the general similarities between the equivalence reactions of the normal and the postoperative animals, three of the tests, D, H and I, did differentiate between the two groups. Normal hedgehogs, for example, found both test H and test I equivalent, whereas for the postoperative animals only the test which included the original positive training stimulus was equivalent. When the negative training stimulus consisting of horizontal or vertical stripes was paired with a single horizontal or vertical line, the postoperative animals responded at a chance level. The fact that the same single lines were found equivalent when paired with a second single line as in tests A and B suggests that a property shared by the positive and negative training stimuli such as "heterogeneous" or "striped" competed with line orientation in determining the responses of the postoperative animals on these tests.

The interrupted stripes in test D were designed to reveal possible visual field defects by determining whether it was necessary for the animals to follow a border of a stripe to recognize its orientation. In general, the reactions of the postoperative animals to test D supported the idea that the operated cases suffered a sensory deficit.

Whereas four normal hedgehogs responded according to the orientation of the dotted lines on this test, three of the five postoperative animals tested scored at a chance level (Postoperative Cases 46, 43, 47, Figs. 25, 28, 29, Pages 85, 91, 93). On the other hand, the two postoperative animals which responded differentially to the dotted stripes, Hedgehogs 44 and 29 (Figs. 26, 27, Pages 87, 89), provide further evidence that the cytoarchitectonic visual area and not the total projection target of the lateral geniculate is the critical unit for pattern discrimination in this species. These two cases had the largest proportion of the cyto-architectonic visual area spared among the postoperative animals which relearned. At the same time, Hedgehog 29 possessed one of the largest lesions in terms of damage to the projection target of GL in the surrounding regions of cortex (Figs. 39-40, Pages 114, 115).

The question of the function of the projections of the lateral geniculate neurons to the surrounding regions of cortex remains unanswered by the equivalence tests. Although many of the animals with large lesions which extended well beyond the boundaries of the cytoarchitectonic visual area had severe relearning deficits, the results obtained from the equivalence tests were remarkably similar to those obtained from the less retarded animals with much

smaller ablations. It is tempting to speculate, therefore, that the retarded animals which were able to maintain an above chance level of performance but not reach criterion on the pattern discriminations suffered from a type of learning deficit in addition to a simple sensory loss. Since, however, the projections of the lateral geniculate overlap extensively with those of the lateral nuclei, L and LP, in the regions surrounding the cytoarchitectonic visual area, it is impossible to estimate with certainty the contributions of each to the deficit.

DISCUSSION

The lack of marked differentiation in the hedgehog thalamus and cortex suggests that the brain of this animal has undergone relatively little change since the origin of mammals. By comparing more advanced species with the hedgehog it should be possible therefore to determine which features of the thalamus and cortex have changed and which have remained stable in mammalian phylogeny. Consequently, the primary significance of the present experiments lies in the pattern of similarities and differences revealed between the hedgehog and other mammals.

The Evolution of the Lateral Geniculate and Visual Cortex

The lateral geniculate of the hedgehog shows few signs of internal differentiation into layers and consists of a homogeneous population of neurons resembling in size and shape the cells found in the adjacent thalamic nuclei. Anatomical studies of other mammalian orders such as the

primates and carnivores have shown, in contrast, that a lateral geniculate differentiated into distinct layers, often consisting of several cell types, is a common feature among mammals. Our own unpublished observations indicate that a distinctly layered lateral geniculate can be found in a rodent (the squirrel), the tree shrew, and even in advanced marsupials such as the wallaby. Comparisons of the lateral geniculates in these forms with the undifferentiated lateral geniculate found in primitive species such as the hedgehog suggest that layering in this structure was not present in ancestral mammals but instead was achieved independently by many different groups.

The differences found among mammals in the detailed relations between the lateral geniculate layers and the distribution of optic tract input from the two eyes support the conclusion that the differentiation of this structure was not a feature of ancestral mammals. In the six layered lateral geniculate of higher primates, for example, the input from the contralateral eye terminates in the two outside layers, 1 and 6, and in one medial layer, 4 (Le Gros Clark, 1959). In *Tupaia glis*, the distribution of terminations is almost completely reversed; the contralateral input terminates exclusively in the inside layers, 2 and 4, whereas the outside layers, 1 and 5, are devoted to fibers from the ipsilateral

eye (Glickstein, Calvin, and Doty, 1966). In the five layered lateral geniculate of the phalanger, still a third arrangement is found. The ipsilateral and contralateral inputs alternate in layers 1 to 4 whereas layer 5 receives bilateral input (Packer, 1941). Such differences in detailed organization constitute strong comparative anatomical evidence confirming that these superficially similar structures have indeed differentiated independently many times in mammalian phylogeny.

The cytoarchitecture of the visual area in the hedgehog suggests that this region of the cortex also has been the site of considerable internal differentiation in several different mammalian lines. In the hedgehog the visual area is remarkably undifferentiated and often fades without distinct boundaries into the surrounding cortical regions. There was no evidence in the cell stained sections through this region of a differentiation of layer IV into sublayers corresponding to those which characterize the striate cortex of higher primates. The primates, however, are not the only mammals with distinct internal differentiation in layer IV of visual cortex. Both the tree shrew and the squirrel possess similar sublayers (Le Gros Clark,1925; Hudgins, Hall and Diamond, unpublished observations). Evidently, as in the case of the lateral geniculate, this structure has undergone similar elaborations independently in different

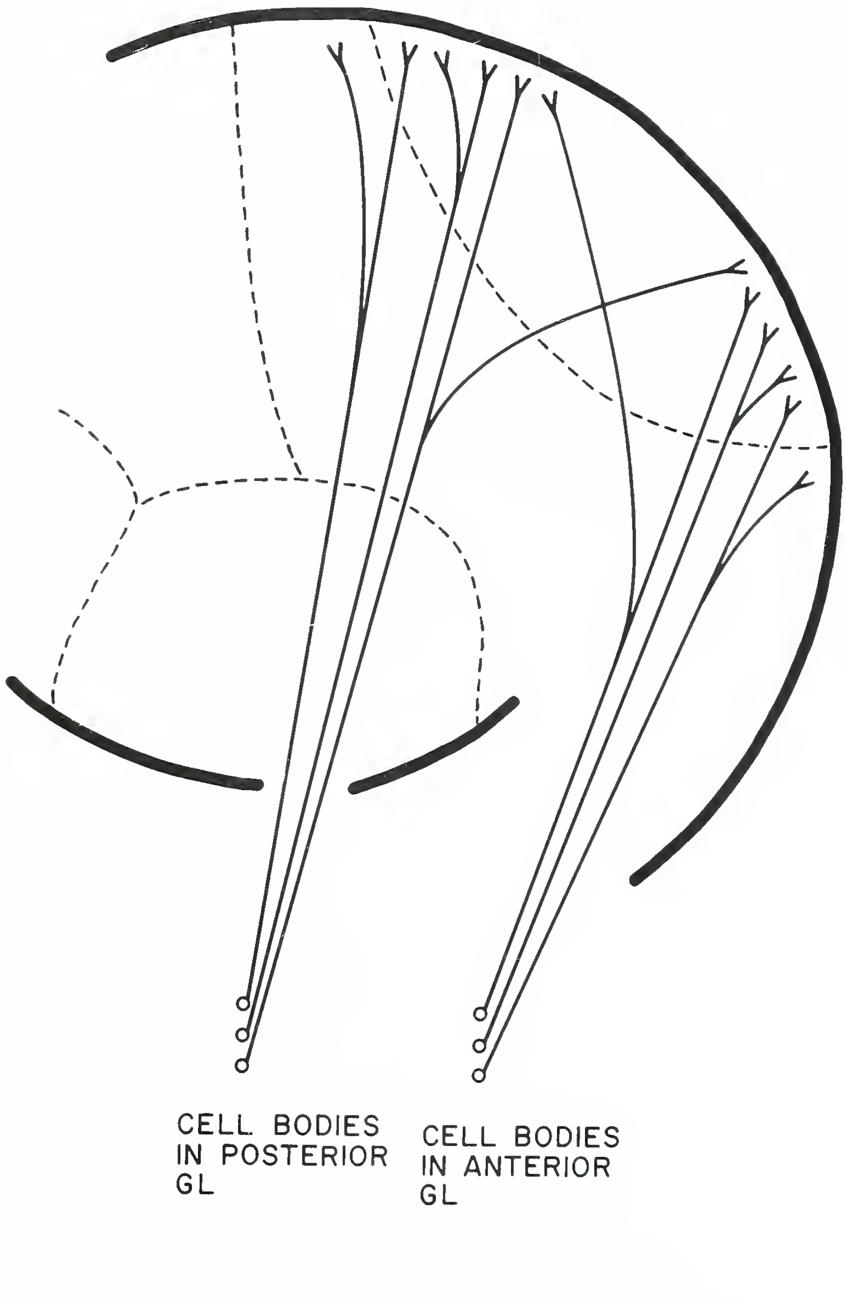
mammalian lines. Whatever are the functional achievements which correspond to these developments in the lateral geniculate and cortex, they apparently represent accomplishments which had adaptive value for a wide range of different habitats rather than responses to a particular species specific ecological requirement.

The Evolution of Geniculo-Cortical Projections

The results of the retrograde degeneration analysis of the projections to the visual area in the hedgehog indicate that this structure is homologous to the region defined as visual cortex in other mammals such as the rat, rabbit, opossum and tree shrew (Lashley, 1934b; Bodian, 1935; Rose and Malis, 1965; Snyder et al., 1966). Thus, in terms of topography of the projections, the relations between the lateral geniculate and the visual area are similar in all of these species. The posterior lateral geniculate projects to anterior visual cortex whereas the anterior part of the lateral geniculate projects posteriorly. Also, in all of these species, the dorsal lateral geniculate projects laterally and the ventral part medially. On the basis of these similarities between many genetically divergent species, it appears that the same organization was already present in the ancestral mammals.

On the other hand, the projections of lateral geniculate neurons appear to be much more widespread in the hedgehog than in more advanced mammals. Punctate visual cortex lesions in species such as the rat, tree shrew and monkey result in restricted zones of severe degeneration in the lateral geniculate (Lashley, 1934b; Snyder, unpublished experiments; Polyak, 1933). To produce degeneration of comparable severity in the lateral geniculate of the hedgehog, large lesions which extended outside the boundaries of the visual area had to be made. With respect to the widespread projections of lateral geniculate neurons, the hedgehog closely resembles the opossum. Figure 56 is a model which was developed to illustrate for the opossum how the projections of the lateral geniculate to visual cortex could be topographically organized yet at the same time diffuse. Essentially the same organization was found in the hedgehog except that the collateral projections outside of the visual area appeared to be even more widespread. Thus massive lesions extending at least as far laterally as the auditory area appeared to be necessary to produce severe degeneration. The contrast between the thalamo-cortical connections in primitive forms such as the hedgehog and the opossum with those found in higher mammals suggests that the evolution of essential from sustaining type projections represents still a third general trend in the

Figure 56. Schematic Representation of the Projections of the Lateral Geniculate in a Primitive Mammal (Diamond and Utley, 1963). The Figure is intended to indicate how the projections of the lateral geniculate can be widespread yet topographically organized. Lesions in the anterior visual area, for example, will produce moderate degeneration in posterior GL and slight degeneration in anterior GL. To produce severe degeneration it is necessary to remove both the striate area and the surrounding cortex.


CELL BODIES IN POSTERIOR GL
CELL BODIES IN ANTERIOR GL

evolution of the thalamus and cortex which was shared by many different lines of descent.

The Anatomical Basis for Pattern Discrimination in the Hedgehog

In view of the diffuse projections of the lateral geniculate to cortex in the hedgehog, the expectation at the outset of the ablation experiments was that massive lesions which included most of the posterior neocortex would be necessary to eliminate pattern discrimination. This expectation appeared to be confirmed by the experimental results in the first few cases studied. Hedgehogs with extensive lesions including cortex from the medial wall to regions as far lateral as the auditory area were still able to discriminate simple patterns at levels well above chance. At the same time, retardation on these tasks appeared to be correlated with the size of the cortical lesion.

The final experimental results, however, supported an entirely different conclusion. The anatomical studies provided a cytoarchitectonic definition of the visual area, and in the later behavioral cases the goal was to make lesions restricted to this region. The lesions which completely removed the cytoarchitectonic visual area were found to produce a permanent inability to distinguish even the most

simple patterns even though large portions of the total projection target of the lateral geniculate were spared. On the other hand, following enormous lesions which spared a small portion of the cytoarchitectonic visual area, the reverse was true; although often retarded with respect to normal hedgehogs, the animals were able to discriminate patterns. Evidently, a precise relation between this cortical subdivision and pattern discrimination was established very early in the history of mammals. It is hard to resist drawing attention to the lesson to be learned from this turnabout: the finding of a correlation between the lesion size and the severity of the deficit may result from ignorance of the relevant anatomical unit.

The Relation between the Hedgehog and Other Mammals

The definition of the structural unit for pattern discrimination in the hedgehog provides an opportunity for deciding which features are stable and which are divergent in the organization of the visual system in other mammals. The most influential experimental investigations of the visual system have been Lashley's extensive series of anatomical and behavioral studies of the rat. Of the eighteen papers published by Lashley on visual mechanisms

in mammals, eleven were concerned with the anatomy and function of the geniculo-striate system in the rat (Lashley, 1930, 1931, 1934a, 1934b, 1935, 1937a, 1937b, 1939, 1942; Lashley and Frank, 1932, 1934). The results of Lashley's inquiry indicate that the organization of the visual system in the rat is remarkably similar to that which already had been established at the earlier stage of mammalian evolution approximated by the hedgehog. On one hand, pattern discrimination following cortical lesions in the rat was found to be precisely dependent upon the sparing of at least a small remnant of the striate area. A sector of cortex in the striate area which received the projections of only 2% of the neurons normally found in the lateral geniculate was sufficient to maintain pattern discrimination (Lashley, 1939).

On the other hand, the removal of large amounts of extrastriate cortex - either alone or together with portions of the striate area - failed to eliminate pattern discrimination (Lashley, 1931; Lashley and Frank, 1934). One possible exception to the conclusion that extrastriate cortex plays no role in pattern discrimination, however, was an ambiguity concerning a region of cortex located immediately lateral to the visual area. The animals which relearned pattern discriminations were discovered to have lesions which spared

this lateral cortex as well as portions of the striate cortex. At the same time, all of the lesions which abolished pattern discrimination included at least small amounts of this area. Although lesions are rarely confined precisely to anatomical borders in ablation experiments, since the removal of extrastriate cortex has been found necessary to eliminate the ability to discriminate patterns in at least one species, the cat, the results of Lashley's investigation of this lateral region are important for the conclusion that the organization of the visual system in the rat resembles that found in the hedgehog (Doty, 1961).

Lashley raised two possibilities to account for the severe deficits which were produced by the ablation of lateral cortex (Lashley and Frank, 1932). First, the area itself may have an important role in mediating pattern discriminations. Secondly, the severe deficit which results from lesions in this area may be due to undercutting the underlying optic radiations. In a series of experiments, Lashley found that the ablation of lateral cortex alone without undercutting had little or no effect on learning pattern discriminations (Lashley and Frank, 1932). If the destruction of the area was accompanied by undercutting, on the other hand, the animal suffered a severe deficit even if large portions of the visual area were spared (Lashley, 1931;

Lashley and Frank, 1934). Analysis of the thalamus, however, indicated that the undercutting produced severe degeneration in the lateral geniculate (Lashley and Frank, 1934). Since all of the optic radiations passed immediately under the area, in many cases lesions almost completely outside of the striate cortex produced severe degeneration throughout the lateral geniculate and, at the same time, permanently eliminated pattern discriminations (Lashley and Frank, 1934). The fact that the sparing of the lateral area was common to the animals which relearned apparently reflected that this is the only cortical region where a restricted cortical lesion which undercuts fibers results in severe degeneration throughout the lateral geniculate. Most important, however, is the fact that even small lesions, which removed very little of either the striate area or the lateral region but interrupted the optic radiations, produced degeneration throughout the lateral geniculate and eliminated pattern discrimination (Lashley and Frank, 1934, see cases 7 and 8, for example). In terms of our present knowledge of the effects of small cortical lesions, it is unlikely that the amount of lateral area removed in these cases made a significant contribution to the severity of the deficit. On the basis of the correlations between the visual deficit with the amount of striate area removed, on one hand, and with the amount of damage to the

optic radiations following lesions in the lateral area, on the other hand, Lashley concluded that only the geniculo-striate system was essential for pattern discriminations in the rat (Lashley, 1931; Lashley and Frank, 1934; Lashley, 1939). Since the collateral projections of the lateral geniculate outside of the visual area in the hedgehog are insufficient to maintain pattern discriminations, the results obtained from these two species appear similar. Evidently, in each animal highly restricted cortical lesions eliminate the ability to discriminate patterns.

Experimental ablation studies indicate that the striate area is also the structural unit for pattern discrimination in the monkey (Klüver, 1942; Denny-Brown and Chambers, 1955). In a classical experiment, Klüver (1942) demonstrated that monkeys deprived of the striate area could distinguish only differences in total luminous energy. Although Klüver never reported his histological results, a more recent study has confirmed that the removal of the striate area alone eliminates pattern vision in the monkey (Denny-Brown and Chambers, 1955). Therefore, in terms of the dependency of pattern discrimination on the striate area, it appears that the basic organization of the visual system which was achieved early in evolution by

ancestral mammals is common to species as diverse as the rat and monkey.

The question which remains is whether any deviations from this basic plan exist. The results of ablation experiments in the cat and tree shrew, for example, indicate that the organization of the visual system may not be the same for all mammals (Doty, 1961; Snyder et al., 1966). Comparison with the hedgehog suggests that the visual system in each of these species represents the product of a divergent trend in mammalian evolution. The studies of the cat indicate that extrastriate as well as the striate cortex has an important role in mediating pattern discrimination in this species (Doty, 1961). To completely eliminate pattern discrimination a large lesion is necessary which includes, in addition to the striate area, most of the cortex as far forward as the middle suprasylvian gyrus. Recent anatomical experiments indicate that the lateral geniculate projects extensively to these extrastriate regions in the cat, including a region on the banks of the suprasylvian gyrus. However, unlike those in the hedgehog, the extrastriate connections in the cat appear to include, at least in part, the essential projections of restricted sectors of the lateral geniculate rather than the collaterals of the same axons which project to the striate area (Sprague,

1965; Glickstein *et al.*, 1967). The ability of the cat to discriminate patterns in the absence of the striate area, therefore, may reflect a special elaboration and organization of the extrastriate connections of the lateral geniculate.

The tree shrew also retains the ability to discriminate patterns after total striate ablations (Snyder *et al.*, 1966). In contrast to the cat, however, enormous lesions which remove almost the entire posterior neocortex still fail to eliminate the ability to distinguish patterns in this species (Snyder, unpublished experiments). The suggestion is that a non-cortical structure such as the remarkably well developed tectum may be sufficient to maintain these functions in the absence of striate cortex.

Conclusions

The preceding discussion indicated that, between advanced species, striking similarities such as layering in the lateral geniculate and in layer IV of the striate cortex exist which were not present in the common ancestor. These similar elaborations of the visual system represent the products of parallel trends in evolution which were shared by many lines of mammalian descent. The discussion also indicated, however, that there are important species

differences such as the role of the striate area in mediating pattern discrimination. These differences are apparently the result of divergent trends in mammalian evolution. Both of these evolutionary processes, divergent and parallel, have important implications for the understanding of cortical development.

The finding of parallel evolution, for example, indicates that there must be general relations between structures and functions in the cortex which apply to all mammals. The problem is to determine whether these general relations will also explain the apparent differences between species. If we knew the functions of the tectum in the hedgehog, for example, then we might also know why a particularly elaborate tectum such as that found in the tree shrew can sustain pattern vision in the absence of striate cortex. At present, however, our analysis has not gone so far as to permit any speculation concerning the functional significance of species variations in neural organization. Understanding the general principles of cortical organization depends on a prior description of the similarities and differences between mammals and, by comparing primitive and advanced species, knowledge of the extent to which the elaboration of structures has followed parallel or divergent courses in the evolution of mammals.

SUMMARY

The hedgehog was selected for an anatomical and behavioral investigation of the visual system because, in terms of the expansion and internal differentiation of its dorsal thalamus and neocortex, this animal appears to have retained a remarkably primitive level of development. By study of a primitive mammal, the hope was to provide a basis for understanding the phylogenetic significance of the similarities and differences found among higher mammals in the anatomical and functional organization of the visual system.

In the anatomical experiments, the visual cortex was defined in terms of cytoarchitecture; the cortical projections of the lateral geniculate to this region were then studied in fourteen hedgehogs by the method of thalamic retrograde degeneration. The lateral geniculate was found to project to the cytoarchitectonically defined visual area in a topographic manner. At the same time, individual neurons in the lateral geniculate appeared to have diffuse cortical terminations

which included extensive regions of the cortex surrounding the visual area. Thus small lesions in the cytoarchitectonic visual area produced widespread but slight degenerative changes in the lateral geniculate. The severity of the degeneration increased with the size of the cortical removal in this region. The most severe degeneration produced in the lateral geniculate, however, was present only after large lesions which extended considerably beyond the boundaries of the visual area.

The purpose of the behavioral experiments was to determine by means of the ablation method the structural unit for pattern discrimination in the hedgehog. Ten hedgehogs were trained to pattern discrimination problems before and after bilateral cortical ablations. The major finding was that despite the widespread projections of the lateral geniculate, pattern discrimination in the hedgehog after cortical surgery is dependent upon the survival of at least a small remnant of the cytoarchitectonic visual area. Complete removal of this area resulted in a permanent inability to discriminate patterns even if, at the same time, the ablations spared large portions of the total projection target of the lateral geniculate. The conclusion was that pattern discrimination had become precisely dependent upon this cytoarchitectonic region at an early stage in the evolution

of mammals. One can recognize this prototypic organization in species as diverse as the rat and the monkey.

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